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Dietary and Behavioral Strategies of Neandertals and Anatomically Modern Humans: Evidence from Anterior Dental Microwear Texture Analysis

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DIETARY AND BEHAVIORAL STRATEGIES OF NEANDERTALS AND ANATOMICALLY MODERN HUMANS: EVIDENCE FROM ANTERIOR DENTAL MICROWEAR TEXTURE ANALYSIS

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of the requirements for the degree of
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ABSTRACT

The extreme gross wear of Neandertal anterior teeth has been a topic of debate for decades. Several ideas have been proposed, including the excessive mastication of grit-laden foods and non-dietary anterior tooth use, or using the anterior dentition as a clamp or tool. This second idea has been the most examined, and was taken from analogy of Arctic populations who used their anterior dentition in this manner. However, combining wear variables and examining them in relation to important factors, such as climate, location, and time, has been challenging to incorporate into interpretive models. The present study seeks to better understand Neandertal anterior tooth wear by integrating these factors with the three wear variables known to affect anterior dental microwear signatures: diet, abrasive load, and non-dietary anterior tooth use.

High-resolution casts of 65 Neandertal individuals from 30 sites and 42 anatomically modern humans from 16 sites were scanned for anterior dental microwear textures using a white-light confocal profiler. Using a 100x objective lens, four adjacent scans were generated measuring a total area of 204 x 276 μm. These scans were analyzed using Toothfrax and SFrax software packages. The fossil hominin samples were then compared to several modern human comparative samples.

The Neandertal sample showed significant variation by climate, location, and OIS. The anisotropy and textural fill volume values of the cold-open-steppe Neandertals were significantly lower and higher, respectively, and both attributes were more constricted than those of the warm-woodland Neandertals. This pattern suggests the cold-open-steppe Neandertals may have been using their anterior dentition frequently in

clamping and grasping activities. Variation in heterogeneity and complexity by location and OIS time interval may suggest differences in abrasive loads.

The anatomically modern human sample showed significant variation in heterogeneity 3x3 and 9x9 distribution variance by climate, location, and time, suggesting differences in abrasive loads in each factor. No differences were found in central tendencies for this sample, and the overall signal suggests little non-dietary anterior tooth use was employed. The differences in non-dietary anterior tooth use signals between the two fossil hominins are suggested to be due to differences in tool technology.

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CHAPTER ONE: INTRODUCTION

The unusual and excessive attrition of some Neandertal anterior teeth has been the subject of several decades of research. While some paleoanthropologists suggested it was from the dentition acting as a compensatory mechanism for amputated hands (Stewart, 1959), studies suggested it was due to jaw movements associated with the chewing cycle, while still others offered a combination of dietary and non-dietary causes (Wallace, 1975; F. Smith, 1976; P. Smith, 1976; Wolpoff, 1979).

The most commonly cited and agreed upon explanation is often referred to as the "stuff and cut" method, in which Neandertals would clamp or grasp a piece of meat, and slice a portion close to their lips (Brace, 1967, 1975; Ryan, 1980; Brace et al., 1981). This idea was advocated most strongly by C. Loring Brace, who generated the idea from ethnographic reports of Alaskan Eskimo and Canadian and Greenland Inuit who used their anterior dentition in this manner. The "stuff and cut" scenario has expanded throughout the decades in response to other types of non-dietary anterior tooth use behaviors found in modern human populations, such as animal hide and sinew preparation, basketry tasks, labret use, wood softening, and tool production and retouching (Cybulski, 1974; Lukacs & Pastor, 1987; Foote, 1992; Mayes, 2001).

Each study has added an individual factor that could have affected Neandertal anterior tooth wear; however, none have attempted to combine these factors in a meaningful way. Additionally, there are other dynamics, such as climate, location, and time, which have yet to be integrated into interpretive models. The advent of paleoclimatology, refined lithic and faunal assemblage studies, improved absolute and relative dating techniques, and stable isotope analyses allow for the construction of more complex frameworks. Moreover, these

early studies relied on light or scanning electron microscopy, both of which are subject to methodological limitations. Indeed, the analysis of Neandertal anterior tooth wear is in need of a theoretical and methodological overhaul.

The purpose of this project is to reevaluate Neandertal anterior dental wear by applying a more comprehensive theoretical framework to objective, repeatable, and three-dimensional dental microwear data. Dental microwear texture signals from sixty-five Neandertals are examined under the lenses of climate, site location, and time interval. Moreover, three wear variables, recognized in pilot research to affect anterior dental wear patterns, are integrated into analyses. The Neandertal texture signals are not only compared with an extensive database of thirteen modern human samples, five of which range from the low to high arctic, but also a collection of forty-two anatomically modern humans (AMH). Comparisons between Neandertals and AMH are often made in conjunction with the former's extinction and the latter's cognitive and behavioral superiority, and analyses of anterior tooth use differences can provide a unique view of the Middle-to-Upper Paleolithic transition.

This chapter first provides a brief review of past interpretations of Neandertals in general, along with the Neandertal evolutionary model applied in this project. The advent of the AMH and the spread of the Upper Paleolithic traditions in Eurasia will also be generally addressed, in particular, with how it has been associated with Neandertal extinction. Then, an introduction to the three factors, climate, time interval, and site location, are discussed, along with the methodology employed in this dissertation, dental microwear texture analysis. Next, the three wear variables known to affect anterior dental wear patterns, and results from a pilot study examining the effectiveness of the methodology to incisor teeth are discussed.

This chapter then closes with the four main goals and accompanying hypotheses of the project.

Neandertal fundamentals

Neandertals lived in Western Eurasia during the Middle and Late Pleistocene, with fossil sites extending from Portugal in the west to southern Siberia in the east, and from the Mediterranean to North Europe (Hublin, 2009). The substantial number of Neandertal site assemblages has yielded extensive archaeological, fossil, dental, and even DNA evidence, allowing paleoanthropologists to learn more about them and their relatedness to modern humans than any earlier hominin.

Neandertals are generally associated with the Mousterian lithic industry of the Middle Paleolithic, which predominantly consists of sidescrapers, points, denticulates, knives, and bifacial hand axes and choppers (Mellars, 1996). However, some sites, specifically Arcy-sur-Cure in France and Vindija Cave in Croatia, provide compelling evidence of stone tool imitation of or trade with penecontemporaneous anatomically modern humans (AMH) during the late Middle Paleolithic and early Upper Paleolithic (Hublin et al., 1996; Karavanić and Smith, 1998, 2000; Ahern et al., 2004, see d'Errico et al., 1998 for an opposing view).

There is a suite of skeletal and dental morphological features that define the "classic" Neandertal, with the overall skeleton demonstrating robusticity with thick cortical bone and large muscle and ligament markings (Harvati, 2007). Additionally, the ribcage is broad, the pubic ramis is thin, and the distal limbs are short relative to modern humans (Boulé, 1911-1913; Trinkaus, 1981; Holliday, 1997; Harvati, 2007). The cranium also displays characteristic features, with a large, broad nasal aperture, convex occipital plane (occipital "bun"), and supraorbital torus (see Hublin, 1998 for a complete list). The mandible and

dentition have also revealed autapomorphic features, such as a space between the third molars and ascending ramus of the mandible (retromolar gap), large pulp chambers (taurodontism), and large, shovel-shaped anterior teeth (Trinkaus & Smith, 1985; Trinkaus, 1987).

The overall robusticity, short stature, and cranial and dental traits have most often been suggested to represent a species adapted to cold climates, and Neandertals have even been described as "hyperarctic", although this idea has been challenged (Aiello & Wheeler, 2003; Finlayson, 2004; Rosas et al., 2008). However, biomechanical explanations relating to non-dietary anterior tooth use behaviors, as well as random processes have been presented as alternative ideas (Rak, 1986; Trinkaus, 1987; Hublin, 1998).

As indicated above, paleoanthropologists have had to rely on morphological characteristics to determine the evolutionary trajectory of Neandertals and their inferred differences and/or similarities with modern humans. However, beginning in 1997, several lines of DNA evidence, both mitochondrial and nuclear genomes, have provided an interesting perspective on Neandertal morphological characteristics, as well as their relatedness to modern humans (Krings et al., 1997; Ovchinnikov et al., 2000; Serre et al., 2004; Lalueza Fox et al., 2005; Orlando et al., 2006; Caramelli et al., 2006; Excoffier, 2006; Green et al., 2006; Krause et al., 2007; Green et al., 2010). These studies found a significant amount of variation between Neandertal and modern human DNA genomes; in fact, the variation was great enough to suggest these two hominins were separate species. These analyses, combined with studies of lithic and faunal assemblage differences between the two hominins, helped to support ideas for cognitive and behavioral superiority of the AMH, and

allowed for Neandertal extinction to be explained, at least in part, by their inability to adapt to competition for resources with the AMH.

However, the recent publication of a draft nuclear DNA genome, pieced together from several late Neandertal fossils, provides more detail than ever before (Green et al., 2010). Indeed, this study shows that Neandertals were more closely related to present-day non-Africans than to Africans, with 1-4% of the modern Eurasian genome derived from Neandertals (Green et al., 2010). This suggests the simplest version of the Out-of-Africa hypothesis, in which all modern humans evolved from a small African population and replaced all other hominins without admixture, may not be correct. Moreover, it also provides evidence for some, albeit little, interbreeding between the two hominins, most likely during interaction in the Levant between 100,000 to 50,000 years ago, before the AMH migration into Europe (Green et al., 2010).

Neandertal evolutionary model used in this dissertation

The "tempo and mode" of Neandertal evolution has been hypothesized by several groups of researchers (Dean et al., 1998; Hublin, 1998, 2009; Hawks & Wolpoff, 2001; Rosas et al., 2008). However, this study utilizes the "Accretion Model" framework, and will adopt its premise and terminology (Dean et al., 1998; Hublin, 1998, 2009). The "Accretion Model" postulates that Neandertal craniofacial apomorphies gradually appeared, in mosaic fashion, from the middle of the Middle Pleistocene, through the middle Late Pleistocene, and ending with the "classic" Neandertal of oxygen isotope stages (OIS) 4 and 3 (Dean et al., 1998; Hublin, 1998, 2009). This accretion pattern has been explained by severely cold conditions in Europe during the Pleistocene with resulting geographic isolation allowing Neandertal morphology to become fixed (Hublin, 1998, 2009). Thus, Neandertal

apomorphies are largely due to genetic drift, but adaptation to cold conditions could also be a factor (Hublin, 1998, 2009; Havarti, 2007).

Under this framework, Neandertal evolution is organized in four phases: early-pre-Neandertals (pre-OIS 12-12), pre-Neandertals (OIS 11-9), early Neandertals (OIS 7-5), and classic Neandertals (OIS 4-3) (Dean et al., 1998; Hublin, 1998). The Neandertal specimens used in this study will be organized following this paradigm.

The factors: paleoclimate reconstructions, time intervals, and site locations

Paleoclimate reconstructions have become paramount in fossil hominin research, especially those in relation to Neandertal subsistence and behavioral strategies. Several lines of evidence have been used to reconstruct the climate of Western Eurasia during Neandertal times, including pollen, ice, and deep-sea cores, computer models, fossil gastropods, insects, sea levels, speleothem growth, Paleolithic spur-thighed tortoises, and loess deposit sequences (de Jong, 1988; Cornu et al., 1993; Dansgaard et al., 1993; Guiot et al., 1993; Cheddadi & Rossignol-Strick, 1995; Tzedakis & Bennett, 1995; Van Andel & Tzedakis, 1996; Alfano et al., 2003; d'Errico & Sánchez-Goñi, 2003; Müller et al., 2003; Serangeli, 2003; Speth & Tchernov, 2003; Vaks et al., 2003; Klotz et al., 2004; Gentry, 2005; Spötl & Mangini, 2006; Gómez-Orellana et al., 2007; Burman & Påsse, 2008).

The Pleistocene of Western Eurasia is often characterized as a series of alternating glacial and interglacial time intervals. Although different terminology is used in different places and by different researchers, oxygen isotope (OIS) or marine isotope stages (MIS) are the most commonly used nomenclature (Emiliani, 1955). Odd OIS numbers designate warm interglacials, while even OIS numbers denote colder, glacial periods (Emiliani, 1955; de Jong, 1988). Each OIS stage can then be divided into cold and/or warm periods, referred to

as stadials and interstadials, respectively, and both are referred to by letters (i.e. 5e or 5a) (Shackleton, 1969; de Jong, 1988; Mellars 1996, van Andel, 2003). Thus, OIS 7 and 5 are interglacials, and OIS 6, 4, and 2 are glacial periods. Oxygen isotope stage 3 was originally designated as an interglacial, but paleoclimate reconstructions have shown this period to have sharp, brief oscillations of warm and cold periods (Dansgaard et al., 1993; GRIP, 1993; van Andel & Tzedakis, 1996; van Andel, 2003).

Under the "Accretion Model" framework outlined above, early and classic Neandertals lived from OIS 7 to OIS 3, which spans approximately 240,000 to 30,000 years BP. During this period, climatic conditions within Neandertal distribution fluctuated, and with it, vegetation and animal migratory patterns. Northern European areas would have been more affected by the oscillating climate than southern Europe, especially the Mediterranean and Iberian Peninsula regions (Tzedakis & Bennett 1995; Mellars, 1996; van Andel & Tzedakis, 1996). However, site assemblages demonstrate that Neandertals were able to adapt to these changing conditions, at least until the rapid climate changes of OIS 3. Subsistence strategies among Neandertals must have differed by region, as southern European and Near East populations did not have to adapt to such radically changing vegetation and animal resources as those in the north. Thus, by considering paleoclimate reconstructions, time intervals, and site locations in the analysis of Neandertal subsistence and behavioral strategies, variations among Neandertal populations can be better examined.

Dental microwear texture analyses

Dental microwear is an important avenue of direct dietary reconstruction, and is described as microscopic scratches and pits that are created on an enamel surface due to the fracture properties of food. For example, it has been demonstrated in past molar microwear

analyses that extant primates who regularly consume hard food objects, such as seeds or nuts, display a high amount of pitting on their enamel surfaces (Ungar, 2002; Ungar et al., 2008a). Occlusal molar or labial incisor surfaces are the most commonly examined teeth, although premolars are beginning to be analyzed as well (Grine et al., 2010).

Early research focused on molar microwear features and their relation to jaw movements and food choices (Butler, 1952; Mills, 1955; Butler & Mills, 1959; Baker et al., 1959; Dahlberg & Kinzey, 1962). However, microwear analyses did not become high profile until SEM-based work by Rensberger (1978) and Walker et al. (1978). Walker et al.'s study, for example, showed differences in microwear signatures between hyrax grazers and browsers, and provided evidence of seasonality and turnover in microwear, a phenomenon later called the "Last Supper Effect" (Grine, 1986). Therefore, dental microwear indicates a short-term tooth-use signature.

Several different methodological procedures have been employed in dental microwear research, with variation in type of microscope, magnification used, feature sizes recognized, and feature definition, all of which have made standardization difficult (Teaford, 2007). Moreover, interobserver error rates were high, microscope costs could be expensive, and three-dimensional features were only being viewed in two-dimensional space (Teaford, 2007). Due to these limitations, a repeatable, objective, and three-dimensional approach to dental microwear, dental microwear texture analysis, was developed at the University of Arkansas (Ungar et al., 2003; R. Scott et al., 2005, 2006).

Dental microwear texture analyses have been used in a variety of molar studies documenting differences in three-dimensional textures rather than the traditional two-dimensional "scratch and pit" approach (R. Scott et al., 2005, 2006; Ungar et al., 2007;

Krueger et al., 2008; Ungar et al., 2008a, 2008b; J. Scott et al., 2009; Merceron et al., 2009). The technique accomplishes this by combining white-light confocal profilometry and scale-sensitive fractal analysis, an engineering protocol rooted in fractal geometry (Scott et al., 2006). This combination allows for the characterization of microwear textures through the use of texture attributes, such as complexity (*Asfc*), anisotropy (*epLsar*), scale of maximum complexity (*Smc*), textural fill volume (*Tfv*), and coarse- and fine-scale variants of heterogeneity ($HAsfc_9$ and $HAsfc_{81}$). Definitions of these attributes are presented in Chapter 3. This project is the first to use this approach on fossil hominin incisors.

Wear variables and the application of DMTA to incisors

The application of dental microwear texture analysis to molars has provided interesting and innovative data concerning the dietary preferences and fallback resources of extant and extinct species (R. Scott et al., 2005, 2006; Ungar et al., 2007; Krueger et al., 2008; Ungar et al., 2008a, 2008b; J. Scott et al., 2009; Merceron et al., 2009). Further work testing the applicability of the technique to incisor teeth also demonstrated that dietary and behavioral adaptations can be detected in bioarchaeological samples of known or inferred incisor use (Krueger & Ungar, 2010).

Maxillary central incisors of five modern human samples, represented by high-resolution casts used for a previous study, were selected for preliminary analysis and are currently housed at the US Museum of Natural History in Washington DC. The five samples, Aleut, Arikara, Illinois Bluff, Chinese immigrants, and Puye Pueblo, differed in their dietary and non-dietary anterior tooth use behaviors, and more complete information about each sample can be found in Chapter 3. An overall MANOVA indicated significant differences between the groups in microwear textures, and individual ANOVAs for each

texture attribute showed these groups differed in anisotropy (*epLsar*), textural fill volume (*Tfv*), and heterogeneity 3x3 ($HAsfc_9$).

Anisotropy was interpreted to indicate non-dietary anterior tooth use practices. Specifically, those samples that did practice these behaviors demonstrated significantly lower anisotropy values than those that did not. For example, the Aleut, an arctic sample, and the Illinois Bluff, from Jersey County, Illinois, had significantly lower values than the other three samples. Both the Aleut and Illinois Bluff are recorded as using their teeth in non-dietary activities, such as hide production, wood softening, and tool production (Hrdlička, 1945; Moorrees, 1957; Mayes, 2001).

Textural fill volume also differed between groups. The Aleut and Puye had higher *Tfv* values than many of the other groups. For the Aleut, the combination of low anisotropy and high textural fill volume suggests high magnitude or repetitive loading of the anterior dentition, most likely related to clamping or grasping activities. On the other hand, the high values for the Puye most likely indicate high abrasive density, since this population likely only used these teeth for food acquisition and processing.

Lastly, heterogeneity 3x3 demonstrated significantly different values. Namely, the Puye showed higher values than the majority of the other samples. It was interpreted that heterogeneity is an indicator of high abrasive exposure. Since the Puye were exposed to a wide variety of dietary and/or environmental abrasives, the results are congruent.

Thus, preliminary analyses of incisor microwear textures demonstrated that dental microwear texture analysis can distinguish bioarchaeological samples by their incisors. Moreover, statistical analyses indicated that the groups differed by anisotropy, textural fill volume, and heterogeneity 3x3. These texture attributes recorded not only the application of

non-dietary and dietary anterior tooth use practices within groups, but also indicated high magnitude or repetitive loading of the anterior teeth, as well as abrasive exposure. These analyses will be kept in mind when the bioarchaeological database is expanded from these initial five samples to thirteen, and these thirteen will be integral in the analyses of both the Neandertal and anatomically modern human samples.

Project goals

This project has four primary goals, which are organized within the following hypotheses:

> **H1:** An enlarged sample from a greater variety of bioarchaeological populations will distinguish modern humans by their incisor microwear textures, and will allow for specific texture signals to be associated with non-dietary and dietary anterior tooth use behaviors.

Preliminary analyses demonstrated that five bioarchaeological samples differ in their incisor microwear textures in anisotropy, textural fill volume, and heterogeneity 3x3. The addition of eight samples to the baseline, including Amarna (Egypt), Andamanese (Andaman Islands), Chumash (California), Fuegians (Tierra del Fuego), Nunavut Territory (Canada), Ipiutak (Point Hope, Alaska), Tigara (Point Hope, Alaska), and Prince Rupert Harbour (Canada) will help to solidify the importance of these texture attributes. The addition of the other arctic samples will allow for an in-depth comparison with the Neandertals, especially as these groups range in latitude from the low to high arctic.

The thirteen populations sampled vary in climate, non-dietary anterior tooth use behaviors, dietary strategies, and dietary and environmental abrasive loads. The development of this baseline series will help to identify specific non-dietary anterior tooth use behaviors within these samples, and correlate microwear texture signals with specific behaviors. This will allow for an extraordinary comparison with both the Neandertals and

anatomically modern human sample to better understand the dietary and behavioral strategies of these hominins.

H2: Neandertal dietary and behavioral strategies can be reconstructed by integrating anterior dental microwear texture data with contextual lines of evidence.

Another primary goal of this project is to reconstruct dietary and behavioral patterns of Neandertals across time and space by integrating anterior dental microwear texture data with contextual lines of evidence, such as climate, site location, and OIS interval. The first step in achieving this goal is to better understand the variables associated with the excessive wear of Neandertal anterior teeth, and the second is to assess whether the contextual lines of evidence could have affected Neandertal behavior.

H3: Anatomically modern human dietary and behavioral strategies can be reconstructed by integrating anterior dental microwear texture data with contextual lines of evidence.

An accompanying goal is the dietary and behavioral reconstruction of anatomically modern humans. Including this sample will help to discern possible differences in dietary and/or behavioral strategies among this fossil group as well, and can provide a unique view of the Middle to Upper Paleolithic transition.

H4: Differences in OIS 3 Neandertal and anatomically modern human diets and other behaviors can be reconstructed from anterior dental microwear texture data and contextual lines of evidence.

Several ideas have been proposed concerning the demise of the Neandertals, and many of them include the role of anatomically modern humans. The basic premise is that Neandertals were outcompeted for resources by the cognitively advanced, encroaching AMH and their extensive toolkits (Harvati, 2007). Many others also include the rapidly oscillating

climatic conditions of OIS 3, which resulted in several other Late Pleistocene megafauna extinctions (Stewart et al., 2003, Stewart, 2005). At the other end of the spectrum, some paleoanthropologists propose that Neandertals were just as capable cognitively, had impressive, complex toolkits, and could have contributed to our gene pool (Hayden, 1993; Green et al., 2010). Thus, this study can reveal variation in diet and other behaviors between these two fossil groups, and may shed light on the adaptive differences between Neandertals and AMH.

Organization of the dissertation

This dissertation is composed of seven chapters. The second chapter is an extensive review of the literature. This includes reviews of Neandertal anterior teeth, paleoclimate reconstruction of geographic areas in which Neandertals have been found, dietary and behavioral reconstructions, and dental microware. Chapter 3 describes the fossil and modern human comparative materials scanned for microwear signatures, and also details the method used in this study, dental microwear texture analysis. Chapter 4 offers results and interpretation of the modern human comparative texture data, and Chapters 5 and 6 offer results and interpretations of the Neandertal and AMH texture data. Finally, Chapter 7 synthesizes results, and offers implications and significance of the research, future directions, and concluding remarks.

CHAPTER TWO: LITERATURE REVIEW

Neandertal dental research

Taxonomy models used in Neandertal dental research

Neandertal research has taken many paths throughout the decades; however, their place within our own evolutionary history has remained a main argument within paleoanthropology. Neandertal taxonomy has been subjected to a theoretical tug-of-war from the earliest discoveries of the 19th century. Several European naturalists assumed the Neandertals to be early European ancestors, and labeled them as *Homo sapiens neanderthalensis* (archaic *Homo sapiens*). However, William King, an Irish anatomist, was the first to classify them as *Homo neanderthalensis*, a separate species, in 1864 (Stringer & Gamble, 1993). This dichotomy between species- and subspecies-level classifications continues at present, and is the theoretical foundation for much of the Neandertal skeletal and dental research. Consequently, an understanding of these frameworks is imperative to understand the interpretations of past work.

Although many variations exist, there are three main competing models concerning the evolutionary history of Neandertals. The first paradigm states that Neandertals are direct ancestors to modern *Homo sapiens*, and is often referred to as regional continuity, multiregional evolution, or the candelabra theory (Weidenreich, 1943; Coon, 1962; Brace, 1962, 1964, 1967; Brose & Wolpoff, 1971; Brace et al., 1981; Wolpoff, 1989; Stringer & Gamble, 1993; Wolpoff et al., 2004). The second proposes a separate evolutionary trajectory for Neandertals, with the "classic" Neandertal of OIS 4 and 3 representing an extinct, separate species with little to no genetic admixture with migrating anatomically modern

humans from Africa (Howell, 1952; Howells, 1974; Klein, 2003). This is most often known as population replacement or Out of Africa 2 (Stringer & Gamble, 1993). The third paradigm is intermediate between the previous two, and suggests that modern humans did indeed evolve in Africa, but were able to interbreed with Neandertals (Bräuer, 1989, 1992). This last model is congruent with recent nuclear DNA analyses that suggest that 1-4% of the Eurasian modern human genome is the result of gene flow from Neandertals (Green et al., 2010). These three theoretical models provide the backdrop to many past Neandertal dental studies.

Neandertal dental morphology

Neandertal teeth are similar to those of modern humans. For example, modern human and Neandertal maxillary molars share basic cusp morphology, including the presence of additional features such as a mesiolingual accessory cusp (Carabelli's cusp), mesiobuccal style (parastyle), and distal cusplet (metaconule) (Bailey, 2004). However, several important differences exist, including the relative placement of cusps, cusp angles, and contribution of cusps to overall crown area (Bailey, 2004). Additionally, Neandertal molars are often described as taurodont, or as having large pulp chambers. This was first recognized by Gorjanovič–Kramberger during his examination of the Krapina site in Croatia (Gorjanovič–Kramberger, 1904, 1906).

Neandertal incisors and canines are generally described as having large roots, a high incidence of incisor shoveling, and expanded mesial-distal and labial-lingual measurements, all of which have been used as indicators of wear resistance (Bailey, 2002, 2006; Harvati, 2007; Bailey et al., 2008; Fig. 2.1). The shovel-shape feature is especially dominant in the

maxillary central incisors, and these mesial and distal marginal ridges can even include cusp-like lingual tubercles in its expression (Bailey, 2002; Fig. 2.1). Indeed, they can be and often are scored high on the ASUDAS[1] scale (Bailey & Hublin, 2006; Bailey et al., 2008). Marked labial convexity is also a common trait of Neandertal incisors, and the scores have also exceeded those found on the ASUDAS scale (Bailey, 2000). Moreover, the combination of labial surface curvature and marginal ridges has been shown to differentiate European fossil hominins from their Asian counterparts (Crummett, 1995).

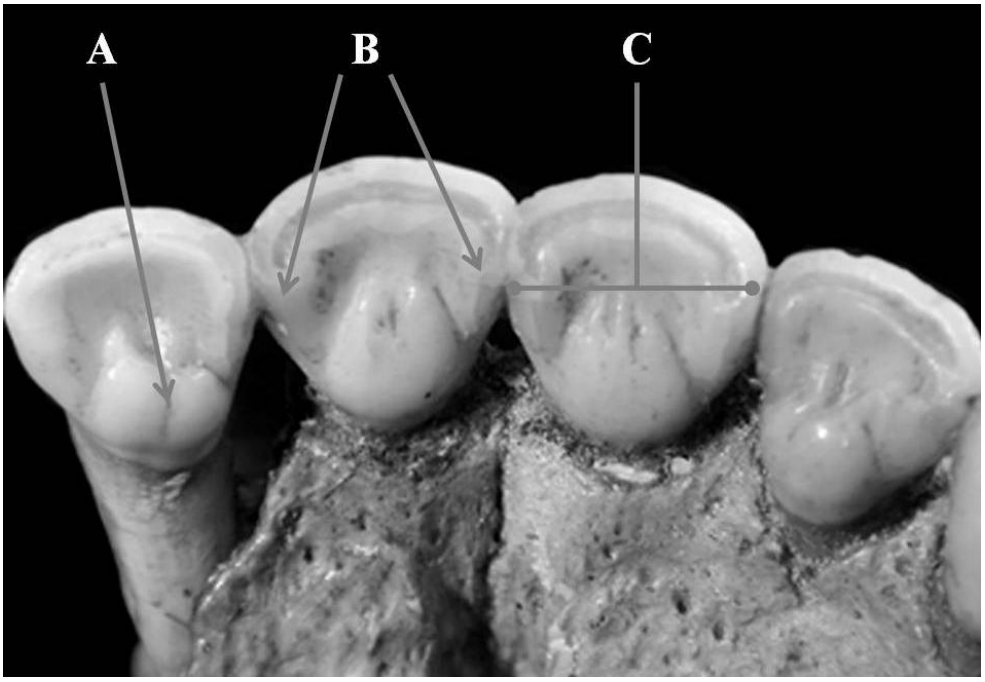

Figure 2.1: Neandertal incisor morphology. Specimen pictured is Krapina Maxilla E. A = Lingual tubercles; B = shoveling, and C = expanded mesial-distal measurement. Photo inspired by Bailey, 2006.

Neandertal tooth size

Although the size of the posterior teeth is within the range of modern humans, the anterior dentition shows a different trend (Puech, 1981; Harvati, 2007). These teeth,

[1] Arizona State University Dental Anthropology System

especially the incisors, have expanded mesial-distal and labial-lingual diameters (Brace et al., 1981; Puech, 1981). Although influenced by gross wear, especially the mesial-distal diameter, these measurements were used to provide evidence for incisor size reduction from Neandertals to modern humans (Brace, 1967; Puech, 1981). Regional continuity was the reigning paradigm, and direct associations between Neandertal robusticity and modern human gracility were emphasized, especially with reference to Bergmann's and Allen's Rules[2]. As a consequence of this model, the impetus for the reduction of the anterior teeth, as well as the cranial-dental complex as a whole, was suggested to be a developing modern culture that no longer required these specialized characteristics for habitual loading of the front teeth (Brace, 1964, 1967, 1979; Trinkaus & Smith, 1985).

Continuing this line of research, Brace et al. (1981) compared the mesial-distal and labial-lingual measurements of Neandertals and modern humans. They found that Neandertal mesial-distal diameters were larger than those of modern humans (1.5 mm for maxillary, 1.3 mm for mandibular). This quantitatively expressed the mesial-distal expansion of the anterior tooth row in Neandertals; however, the labial-lingual diameter was considerably more significant. The maxillary and mandibular sums of Neandertal labial-lingual diameters were 5.7 mm and 6.3 mm (respectively) greater than those of modern humans (Brace et al. 1981). This, according to the authors, provided further evidence that Neandertals were adapted to use their front teeth in activities other than food ingestion, and that the reduction in modern humans was due to cultural advances (Brace et al., 1981).

[2] These rules, which state a correlation between body mass and latitude (Bergmann's Rule) and limb proportions and latitude (Allen's Rule) are only relevant within the same species group. Therefore, in order to apply these rules, Neandertals and modern humans must be members of the same species.

Other studies refuted this claim (P. Smith, 1976, 1977a, 1977b). In a series of carefully constructed analyses, Smith showed that a reduction in functional demands on the teeth did not cause a decrease in overall tooth size through time. In order to estimate the functional demands on the teeth, she first scored the attrition on a six-point scale and compared those scores to tooth size (P. Smith, 1977a, 1977b). The first study demonstrated an inverse relationship between attrition scores and tooth size; that is, attrition increased as tooth size decreased (P. Smith, 1977a). This suggested a consistent functional demand through time (P. Smith, 1977a). The second study examined regional areas for evidence of differences in demands on the teeth (P. Smith, 1977b). Although there was little variation in tooth size by region for the Middle and Upper Pleistocene sites examined, there was significantly more attrition and pathological lesions in the European sample than in the Near East sample during the Würm I-II time period (P. Smith, 1977b). This was attributed to an increase in abrasive loads related to environmental differences (P. Smith, 1977b).

Neandertal dental wear

Neandertal posterior teeth often display extensive wear, with little enamel left on the flat, occlusal surface; however, the unusual wear of the incisors and canines of some has gained more attention. This wear is described as an obliteration of much of the overall tooth crown, but there is an increase in wear on the labial and lingual sides of the incisal edge, creating a labial-lingual rounding effect in some specimens (Stewart, 1958, Fig. 2.2). Stewart (1958) attributed this wear not to chewing food, but to using the anterior dentition as a hand for holding objects. This was described as a compensatory strategy for the Shanidar I specimen he was describing, which lacked a right arm (Stewart, 1958, 1959, Fig. 2.2).

Stewart's idea regarding the Shanidar I specimen led to the most popular idea regarding anterior dental wear of Neandertals. Often referred to as the "stuff and cut" scenario, it describes the use of the anterior dentition as a clamp (Brace, 1967, 1975, 1979; Brace and Molnar, 1967; Brace et al. 1981). This idea proposes that Neandertals used their anterior dentition to clamp down on a piece of meat while they cut a portion close to their lips. This scenario was taken from ethnographic reports of Alaskan Eskimo and Canadian and Greenland Inuit using their front teeth in this manner.

To test this hypothesis, Ryan (1980), Brace's student at the time, conducted a scanning electron microscopy-based anterior dental microwear study of Neandertals. Ryan (1980) suggested that the microscopic flaking and gouging patterns on the Neandertal anterior teeth were similar to those seen in an arctic comparative sample, the Ipiutak from Point Hope, Alaska, which was consistent with a "stuff and cut" interpretation.

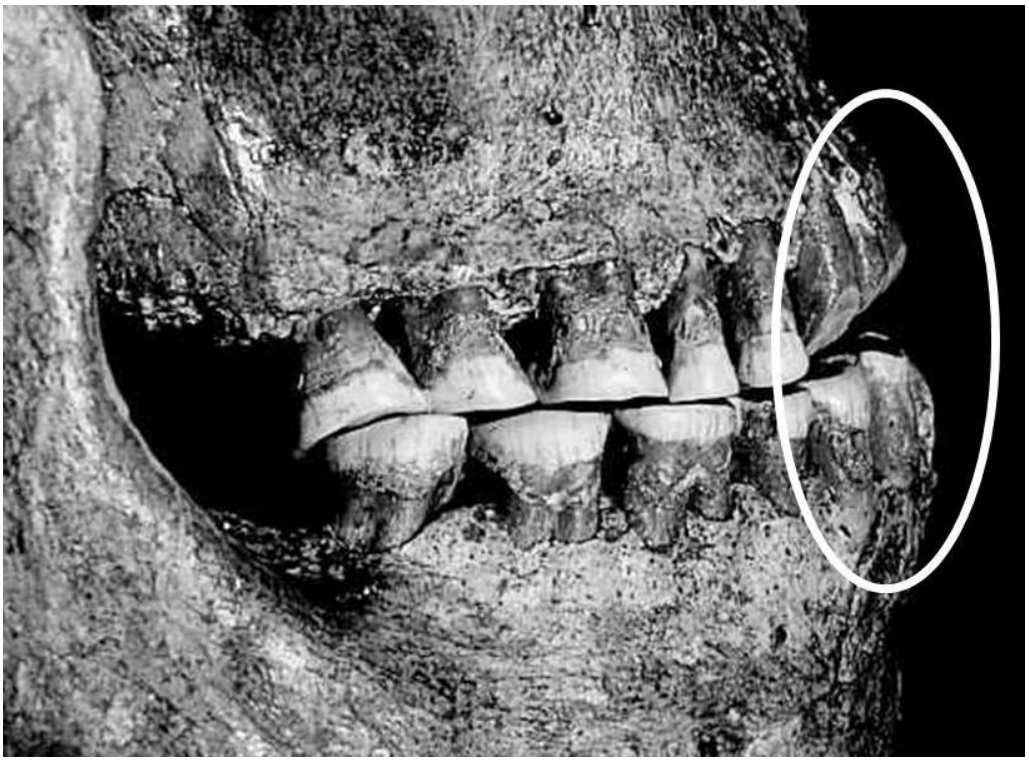

Figure 2.2: Example of labial-lingual rounding found in some Neandertal specimens. Pictured here is Shanidar I from Shanidar Cave in northern Iraq.

The Middle Pleistocene hominin site of Sima de los Huesos, dated to the Accretion Model's pre-Neandertal stage of OIS 11-9, (see Chapter 1) has generated evidence for the antiquity of the "stuff and cut" behavior (Bermúdez de Castro et al., 1988; Fernández Jalvo & Bermúdez de Castro, 1988). Macroscopic striations were observed on the labial surfaces of 13 out of 16 hominin incisors and canines. In order to rule out the possibility of depositional damage, they also examined fossil bear remains (*Ursus deningeri*), and found different striations related to chewing foods with abrasive inclusions (Fernández Jalvo & Bermúdez de Castro, 1988). Moreover, through experimental processes, the authors concluded the striations were most likely caused by stone tools scratching across the labial surfaces. The observational and experimental data allowed the authors to support the "stuff and cut" scenario, suggesting early evidence of this behavioral strategy in European hominins (Bermúdez de Castro et al., 1988; Fernández Jalvo & Bermúdez de Castro, 1988).

Similar macroscopic striations on the labial surfaces of incisors and canines have been found on Neandertal and modern human samples (Lalueza Fox & Frayer, 1997; Bax & Ungar, 1999; Hlusko et al., in review). Although suggested to be useful for determining handedness, the directionality of the labial striations were not found to be correlated with the "stuff and cut" scenario, at least in the modern human samples examined (Bax & Ungar, 1999).

Another idea suggested for the excessive anterior tooth wear was abrasion, or the wear action of foreign objects or dietary abrasives on the teeth (Wallace, 1975; Puech, 1979, 1981). This was proposed after modern human aboriginal skulls, which were also found with rounded anterior teeth, were examined using a light microscope. The rounded edges

presented many fine scratches, and similar scratches were found on the posterior teeth as well. This was interpreted as a clear signal of tiny, firm particles of sand or soil that were most likely introduced with food (Wallace, 1975).

Moreover, a connection was made between rounded teeth and the failure of the maxillary and mandibular incisors to meet in occlusion, often referred to as an anterior open bite (Wallace, 1975). This open bite would exacerbate the problem, as the incisors would no longer be functional to cut off pieces of food; instead, the food would be raked and shredded across the anterior teeth, and soil and sand attached to food would further wear and round them (Wallace, 1975).

However, as Koritzer (1975) pointed out, abrasive agents could also be present on non-dietary items, such as leather, during a production process. Additionally, teeth used as tools must also be used for eating, and molars with pathological lesions would cause the anterior teeth to be favored (Koritzer, 1975; Sakura, 1975). Indeed, F. Smith (1976) stated that a combination of dietary and non-dietary factors most likely caused this unique wear. Clearly, there are many possible factors and agents to consider with this phenomenon.

Biomechanical models for anterior tooth use in Neandertals

The unique combination of Neandertal cranio-dental morphology and anterior tooth size and wear led researchers to hypothesize that the Neandertal face was adapted to high magnitude and/or repetitive loading of the anterior teeth (F. Smith, 1983; Trinkaus, 1983; Rak, 1986; Demes, 1987). However, the posterior position of the zygomatic arch relative to the maxillary molars and the presence of the retromolar space were used as indicators that the masticatory muscles retreated posteriorly relative to the dental arcade, sparking debate about

the biomechanical efficiency (and evolutionary significance) of non-dietary anterior tooth use in Neandertals (Trinkaus, 1987; Smith & Paquette, 1989). Research then shifted to whether the Neandertal face was biomechanically adept or inept at handling high magnitude force loads on the anterior teeth.

Spencer & Demes (1993) completed biomechanical analyses on Neandertal and Alaskan Eskimo crania under the assumption that both groups used their anterior dentition as a tool. These samples demonstrated several biomechanical specializations suggested to be indicative of anterior tooth use, including the anterior migration of the muscles of mastication; however, they also differed in important ways, primarily in relation to the posterior dentition. The most significant difference was that the Neandertal sample demonstrated an anterior migration of the molars in relation to the temporomandibular joint (TMJ), but the Eskimo sample did not (Spencer & Demes, 1993). The combination of the anterior migration of the molars and muscles of mastication in Neandertals indicated a more efficient bite force, and supported the idea that the Neandertal facial design was ideal for heavy and repetitive loading of the front teeth (Spencer & Demes, 1993). This was further supported by additional comparative studies of incisor use, dental microwear, and craniofacial morphology in modern human samples (Ungar & Spencer, 1999; Spencer & Ungar, 2000).

Other paleoanthropologists doubted these claims, as the underlying assumption was that Neandertal and modern human masticatory muscles were structurally similar, and, as a result, physically capable of producing the same amount of force (Antón, 1996). By examining the muscle structure vis-à-vis bony features, one could reasonably predict whether Neandertal muscles were structurally similar or different, and thus, capable of producing less,

similar, or greater bite force than modern humans (Antón, 1996). Results indicated that bony features associated with the masseter, temporalis, and medial pterygoid muscle attachments (adducting muscles of mastication) of Neandertals were slightly larger than those of modern humans; however, this increase was not great enough to produce a higher anterior bite force (Antón, 1996). Repetitive loading, rather than high magnitude loading of the anterior teeth was suggested to be the cause of Neandertal anterior dental wear (Antón, 1996).

Additional data supported the idea that Neandertals were neither capable of nor efficient at extremely high magnitude loading of the front teeth (O'Connor et al., 2005). Force production capability of Neandertals, early modern humans, and recent modern humans, measured as estimates of incisor bite, muscle, and condylar reaction forces, was similar. In fact, incisor bite force in some early modern humans was estimated to be higher than in some Neandertals used in the study (O'Connor et al., 2005). Force production efficiency for these three samples, measured as ratios of force magnitudes[3] and muscle mechanical advantages[4], also demonstrated that Neandertals were neither better nor worse at high bite force efficiency than the modern human samples (O'Connor et al., 2005). These data led the authors to agree with Antón's (1996) conclusions that Neandertal anterior dental wear was most likely caused by repetitive, not high magnitude, loading, and alternative ideas regarding the evolutionary significance of the unique cranial-facial-dental morphology should be explored (O'Connor et al., 2005).

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[3] Efficiency is defined as "the ratio of a designated output to the required input" (O'Connor et al., 2005:135). Outputs are the bite force and condylar reaction force and input is the total muscle force. For an efficient system, the bite force-to-muscle force ratio should be high, whereas the condylar reaction force-to-muscle force ratio should be low.

[4] Mechanical advantage (MA) is defined as the quotient of the bite force lever arm into the muscle force lever arm (O'Connor et al., 2005). A large MA indicates a muscle well-positioned for creating a particular bite force.

Ultimately, most researchers now accept the idea that Neandertals were using their anterior dentitions as a tool, and it seems as though modern human samples from the arctic provide the most appropriate analog to examining this phenomenon. However, several caveats exist. First, while arctic samples are often used as equivalent to Neandertals, most researchers use these groups interchangeably, as if these populations behaved identically through time and space. This project uses five samples that range from the low to high arctic, allowing for a more appropriate and broad-ranging comparison with the fossil sample, as well as identifying differences in tooth use behaviors within the arctic samples themselves. Additionally, past research has not integrated all the variables related to anterior dental wear. It was been demonstrated that incisor tooth wear is a combined consequence of diet, environmental and dietary abrasive loads, and non-dietary anterior tooth use (Krueger and Ungar, 2010). All variables will be be accounted for in determining the causes of Neandertal anterior dental wear in this study.

Paleoclimate Reconstruction

Brief history

Early geologists, such as Lyell and Agassiz, determined that Europe had been subjected to glaciations during the Pleistocene, and even provided approximate timings for them. In 1909, Pench and Brückner provided the most popular system for ice age classification in Europe, called the Alpine System (Stringer & Gamble, 1993). This system, which referred to the four European ice ages as Günz, Mindel, Riss, and Würm, allowed early paleoanthropologists and archaeologists to relatively date lithic and fossil material found in cave sediment sequences (Stringer & Gamble, 1993). Indeed, you can still find references to the Alpine System in paleoanthropology and archaeology.

However, the Alpine System is not without its flaws. Discontinuous sediment sequences, erosion, cryoturbation, and other geologic processes wreaked havoc on attempts to correlate fossil and lithic materials to both dates and climate conditions (Stringer & Gamble, 1993). A method that included undisturbed and continuous data was necessary to advance the field, and so the use of deep-sea cores began in the 1930s (Emiliani, 1955).

Deep-sea sedimentation, while offering the undisturbed and continuous data needed, only provided climate signals of the environments that contributed to the sediments themselves (Emiliani, 1955). The environments that make up the sedimentation, and, indirectly, the climate signal, include the ocean floor, the water column above the floor (especially the euphotic zone[5]), and the nearest land areas (Emiliani, 1955). The most significant environment is the euphotic zone, which contributes calcium carbonate-based skeletons of microscopic animals, or foraminifera (Emiliani, 1955; Stringer & Gamble, 1993).

When alive, foraminifera absorb the two[6] oxygen isotopes found in ocean water, ^{16}O and ^{18}O. While the ^{16}O isotope contains eight protons and eight neutrons, the ^{18}O isotope is two neutrons heavier. This added weight requires more energy for evaporation. Conversely, the lighter ^{16}O isotope is more easily evaporated, and during glacial times, this isotope is readily absorbed and captured in glacial ice, leaving the ^{18}O isotope in the ocean water (Emiliani, 1955; Shackleton, 1969; Stringer & Gamble, 1993). As a result, the $^{18}O/^{16}O$ ratio is high during glacial times, and low during interglacial periods, and the foraminifera document these fluctuations (Cheddadi & Rossignol-Strick, 1995). This is the basis for the

[5] Also known as the sunlit zone, or the depth of the water where enough sunlight allows photosynthesis to occur.
[6] There is also an ^{17}O isotope, but it is very rare.

oxygen isotope stages (OIS), which were not only developed, but also correlated with the Alpine System, by Cesare Emiliani (Emiliani, 1955).

Proxies for climate reconstruction: what kind of information can they tell us?

As briefly discussed in Chapter 1, there are several unique methods for paleoclimate reconstruction, and each one can describe different climate attributes. For example, pollen pulled from deep-sea and terrestrial cores is the most often used proxy, and can provide indirect evidence of vegetation (Shackleton, 1969; de Jong, 1988; Guiot et al., 1993; Cheddadi & Rossignol-Strick, 1995; Tzedakis & Bennett, 1995; van Andel & Tzedakis, 1996; Tzedakis et al., 1997, 2003; Kukla et al., 2002; Müller et al., 2003; Klotz et al., 2004; Gentry et al., 2005; Roucoux et al., 2006; Gómez-Orellana et al., 2007; Fletcher et al., 2010. Speleothems, or stalagmites, stalactites, and flowstones, are quickly becoming more and more common in paleoclimate reconstruction, as they can provide information about vegetation, temperature, and precipitation (Vaks et al., 2003; Gentry et al., 2003, 2005; Spötl & Mangini, 2006; Hodge et al., 2008; Meyer et al., 2009). Moreover, speleothems can be dated using the uranium/thorium (U/Th) radiometric technique (Spötl & Mangini, 2006). In addition to paleoclimate signals in deep-sea cores, $\delta^{18}O$ found in fossil gastropods, such as *Littorina littorea* and *Stombus bubonius*, can offer sea-surface temperature (SST) and sea-surface salinity (SSS) measures (Cornu et al., 1993; Burman & Påsse, 2008).

Each individual proxy can provide important clues regarding past climate conditions; however, each has its own drawbacks. As a result, most research uses a multiproxy approach to mitigate these obstacles. For example, pollen sequence analysis is undoubtedly the most frequently used technique. Pollen grains are durable, preserve for thousands of years, and are

easily identified (Guiot et al., 1993). However, this technique cannot be used in extreme cold events, and changes in the pollen spectrum composition, which would indicate climate change, can be caused by other factors (de Jong, 1988; Guiot et al., 1993). These factors include the effects of wind and water, changes in soil composition, and differential preservation or production of pollen grains (de Jong, 1988; Guiot et al., 1993; Cheddadi & Rossignol-Strick, 1995). In spite of this, researchers have used complementary lines of evidence, such as insect remains, faunal remains, and loess deposits, to verify or calibrate the pollen evidence (Guiot et al., 1993; Speth & Tchernov, 2003; Gentry, 2005). In accordance with the majority of paleoclimate research, the following reconstructions of Western Eurasia during oxygen isotope stages (OIS) 7-3 are based on a multiproxy approach.

Paleoclimate reconstructions of OIS 7-3 in Western Eurasia

OIS 7 (245-186 kyr BP)

Oxygen isotope stage 7 is known as the penultimate interglacial, and was divided into three sub-stages: 7a, 7b, and 7c, with the intermediate sub-stage representing a rapid, ice-age pulse (Ruddiman & McIntyre, 1982; Gamble, 1999). However, as techniques have improved and evidence accumulated from this enigmatic time period (especially from southern Europe), paleoclimatologists now recognize five sub-stages: 7e, 7d, 7c, 7b, and 7a (Cheddadi & Rossignol-Strick, 1995; Tzedakis & Bennett, 1995; Tzedakis et al, 1997, 2003, 2004; Hodge et al., 2008; Roucoux et al., 2006, 2008). As acknowledged above, OIS 7 is designated as an interglacial period, however, sub-stages 7d and 7b are designated as stadials, whereas the other three sub-stages are warmer periods (Tzedakis et al, 2004; Hodge et al., 2008; Roucoux et al., 2006, 2008).

Sub-stage 7e is the earliest, and Antarctic ice and French terrestrial cores suggest the temperatures during this interval were higher than those in the Holocene, and sea levels were approximately the same (Tzedakis et al., 2004). Temperate forests developed in Iberia with both deciduous and Mediterranean forms of *Quercus* (oak) dominating the pollen record (Cheddadi & Rossignol-Strick, 1995; Tzedakis et al., 2004). Similar taxa are identified in Greece, with deciduous *Quercus* expanding after initial populations of *Juniperus*,(juniper) *Betula*, (birch) and *Pinus* (pine) had begun to grow (Roucoux et al., 2008). However, this short warming period of approximately 4,000 years was followed by a rapid decrease in temperature, which led to a gradual decline in both climate, effective precipitation, and forest cover (Tzedakis et al., 2004; Hodge et al., 2008).

Sub-stage 7d was an extremely cold, dry stadial (Tzedakis et al., 2003; Roucoux et al., 2006; Hodge et al., 2008). Ice cores from Antarctica and the North Atlantic provide evidence for low global temperatures, low glacial sea-surface temperatures, and large ice volumes (Roucoux et al., 2008). This coincides with marine pollen core sequences indicating a pronounced reduction in arboreal taxa and expansion of open, steppe vegetation in Portugal (Tzedakis et al., 2004; Roucoux e al., 2008). In Greece and other areas of the Mediterranean, temperate forests of the beginning of 7e completely disappeared, and a semidesert, represented by arid taxa, such as *Artemisia* (sagebrush, etc.) and *Ephedra* was widespread (Cheddadi & Rossignol-Strick, 1995; Tzedakis et al., 2003; Roucoux et al., 2008).

Sub-stage 7c is the most discussed interval because it is the longest, had the highest summer insolation[7] (solar radiation), had the peak effective precipitation, and had the widest

[7] Although 7c has the highest summer insolation, it did not have the highest overall temperature. The 7e interval had the highest overall temperature. However, the high

expansion of forest cover than any other period in stage 7 (Cheddadi & Rossignol-Strick, 1995; Tzedakis & Bennett, 1995; Tzedakis et al., 1997, 2003; Hodge et al., 2008). In fact, pollen sequences in Portugal and Greece demonstrate that 7c was the most diverse in forest development compared with any of the other intervals (Tzedakis et al., 2004; Roucoux et al., 2006, 2008).

Deep-sea cores from coastal Portugal reflect a climate of Mediterranean taxa and *Corylus* (hazel), whereas lake cores from Greece show *Pinus*, (pine) *Quercus*, (oak) *Ulmus*, (elm) *Pistacia*, *Tilia*, (lime or linden) *Corylus*, among other temperate taxa (Tzedakis & Bennett, 1995; Tzedakis et al., 2004; Roucoux et al., 2006, 2008).

Sub-stage 7b is tentatively labeled as a stadial, although it did not reach the same cold and arid conditions as 7d (Roucoux et al., 2006). Sea-surface temperatures dropped and ice volume increased only slightly, with some open-steppe taxa appearing, but temperate species still lingering across the majority of southern Europe (Tzedakis et al., 2003; Roucoux et al., 2006, 2008). Evidence from Greece suggests a short reduction in temperate arboreal populations, with an increase in steppe vegetation such as *Betula* (birch), and *Quercus* (oak) (Roucoux et al., 2008).

Sub-stage 7a is similar to 7e and 7c in overall temperate conditions, although 7a and 7c did not reach the overall high temperatures of 7e (Tzedakis et al., 2003; Hodge et al., 2008). In Portugal, pollen evidence illustrates an expansion of Mediterranean taxa at first, then a decline in arboreal populations, with a subsequent development of *Quercus* (Roucoux et al., 2006). Pollen records from Greece indicate a forested interval, with a primary expansion of *Pinus* and *Betula*, a small amount of *Juniperus*, and a secondary development

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summer insolation of 7c has been credited as being the primary catalyst for the expansion of the temperate forests during this time (Tzedakis et al., 2003).

of *Quercus*, *Carpinus* (hornbeam), and *Abies* (fir) (Roucoux et al., 2008). Heathland, a dwarf-shrub habitat, then marks the transition from stage 7 to stage 6 (Roucoux et al., 2006).

OIS 6 (186-127 kyr)

Oxygen isotope stage 6 is also known as the penultimate glacial period. Although this stage is not divided into sub-stages, there is evidence of some climate pulses (Tzedakis et al., 2003; Hodge et al., 2008). The beginning of OIS 6 brought a reduction in sea-surface temperatures (SST) and an increase in global ice volume (van Andel & Tzedakis, 1996; Roucoux et al., 2006). Deep-ice cores from Antarctica buttress this pattern, as the isotopic temperature sequence recorded temperatures that rivaled those of the last glacial maximum (LGM) (Jouzel et al., 1993). Carbon dioxide and methane concentrations, which are positively correlated to temperature, are also low and comparable to those of the LGM (Jouzel et al., 1993).

Regions north of the Alps would have reflected these extremely cold conditions, with continental ice sheets reaching nearly maximum expansion in northern Europe, polar desert near the ice margin, and tundra-steppe vegetation taking over the landscape just south of the polar desert (Mellars, 1996; van Andel & Tzedakis, 1996). Pollen from grasses, sedges, and *Artemisia* are found in terrestrial sequences, and tundra-adapted insect assemblages (van Andel & Tzedakis, 1996). Several terrestrial pollen sequences from France show a marked reduction in temperature and precipitation (van Andel & Tzedakis, 1996).

Deep-sea cores from coastal Portugal illustrate a marked reduction in forest and heathland, and a development of steppe and juniper trees, indicating a shift to cold and dry conditions (Roucoux et al., 2006). Speleothem stable carbon isotope records from Spain indicate a reduction in effective precipitation at the onset of OIS 6, but a short pulse of

warmer and wetter conditions at approximately 180 kya (Hodge et al., 2008). After this pulse, sea-surface temperature, precipitation, and vegetation cover continued to decline, with concomitant cold, arid conditions in the western Mediterranean (Hodge et al., 2008). Indeed, sea-surface temperatures were estimated to be approximately 8-10°C (46-50°F) at the peak of OIS 6 glacial conditions (Hodge et al., 2008).

Evidence from the eastern Mediterranean mirrors that from the western Mediterranean, as pollen sequences suggest a semidesert environment, with *Artemisia*, chenopods, and grasses dominating the landscape, and some glacial refuge areas where oak could survive (Cheddadi & Rossignol-Strick, 1995; van Andel & Tzedakis, 1996). Sea-surface temperatures are estimated to have been 5°C (9°F) colder than in the Holocene (van Andel & Tzedakis, 1996).

After this peak, a slight increase in temperature occurred at 150 kya, with SST values doubling in coastal Portugal (Hodge et al., 2008). Moreover, arboreal pollen percentages in Greece increased slightly, with *Pinus* dominating the interval, along with some temperate trees (Tzedakis et al., 2003). However, another cold, dry pulse at approximately 133 kya is documented in the western Mediterranean, and resulted in reduced SST once again (Hodge et al., 2008). It is under these cold and arid conditions that the last interglacial, known as 5e or the Eemian, abruptly began (Stringer & Gamble, 1993; Mellars, 1996).

OIS 5 (127-71 kyr)

Oxygen isotope stage 5 is divided into five sub-stages, 5e, 5d, 5c, 5b, and 5a (Shackleton, 1969). Sub-stage 5e dates from 127-118 kya, and is referred to as the last interglacial period (Mellars, 1996). This sub-stage has been studied extensively because it

provides a possible analogue to future Holocene climate conditions (van Andel & Tzedakis, 1996; Kukla et al., 2002).

The beginning of sub-stage 5e is clear and abrupt in paleoclimate proxies, with a sudden increase in insolation suggested to be the catalyst (Mellars, 1996). Within a few thousand years, temperatures increased by 10-15°C (18-27°F), and global ice volume decreased dramatically (Mellars, 1996; Kukla et al., 2002). Several ice core sequences from Greenland and Antarctica record temperatures that were 2-3°C (3.6-5.4°F) higher than Holocene values and the retreat of the ice sheets suggests sea levels were 5-6 meters higher than at present (Stringer & Gamble, 1993; Mellars, 1996; van Andel & Tzedakis, 1996; Kukla et al., 2002; Shackleton et al., 2003). Indeed, evidence of semi-tropical fauna, such as pond tortoises, elephants, rhinoceroses, and hippopotamuses, are found as far north as England, while arctic fauna, such as the woolly rhinoceroses and mammoths migrated further north (Stringer & Gamble, 1993; Mellars, 1996).

Oxygen isotope ratios from fossil marine gastropods indicate that sea-surface temperatures (SST) in the western Mediterranean were higher than today by 3°C (5.4°F) (Cornu et al., 1993). Northwest Europe $\delta^{18}O$ suggest similar conditions, as fossil marine gastropods from the English Channel and Sweden had summer SST approximately 1-3°C (1.8-5.4°F) higher than today (Burman & Påsse, 2008). Although winter SST for the English Channel were comparable to today's temperatures, those from Sweden were 8°C (14.4°F) higher (Burman & Påsse, 2008).

Pollen sequences from several European areas evince a parallel pattern of closed-canopy forest production, with *Pinus* (pine) and *Betula* (birch) trees appearing first, and then a succession of warm-loving, deciduous trees, such as *Quercus* (oak), *Ulmus* (elm), *Fraxinus*

(ash), *Alnus* (alder), *Corylus* (hazel), and *Taxus* (yew) (Cheddadi & Rossignol-Strick, 1995; Tzedakis & Bennett, 1995; Mellars, 1996; van Andel & Tzedakis, 1996; Kukla et al., 2002; Müller et al., 2003). In southern Europe and the Levantine basin borderlands, evergreen forests with *Quercus* (oak), *Olea* (olive), and *Pistacia* (pistachio) flourished, and the semidesert disappeared with the general warm and wet conditions (Cheddadi & Rossignol-Strick, 1995). The last phase of 5e shows coniferous trees, such as *Picea* (spruce), *Pinus* (pine), and *Abies* (fir) over the majority of Europe (Tzedakis & Bennett, 1995; Mellars, 1996; van Andel & Tzedakis, 1996; Kukla et al., 2002; Müller et al., 2003). Therefore, only at the very beginning and end of 5e would open areas of vegetation replace dense forests (Dansgaard et al., 1993; Mellars, 1996).

The remainder of OIS 5 is identified as the early glacial period, and dates from 118-75 kya (Mellars, 1996). There are four sub-stages: 5d, 5c, 5b, and 5a (Shackleton, 1969). Sub-stages 5d and 5b represent stadials, while 5c and 5a are interstadials (Mellars, 1996). Due to similar conditions found in both stadials and, likewise, in both interstadials, the climate reconstructions for these sub-stages will be combined.

Sub-stages 5d and 5b are also known also as Melisey I and II, respectively, and are glacial intervals (Guiot et al., 1993). The impetus for the transition into stadial conditions is, based on predictions of the Milankovitch cycle[8], a reduction in insolation (Mellars, 1996). The consequence of this decrease in solar radiation was an expansion of continental ice sheets to approximately half the volume as the LGM (Mellars, 1996; van Andel & Tzedakis, 1996). Although these ice sheets would have expanded over northern Europe, the extent of

[8] The Milankovitch cycle (theory) states that changes in the Earth's eccentricity (deviation from a circular orbit around the Sun), axial tilt, and precession (any rotational or orbital pattern change) influence climate patterns (Berger, 1988).

their expansion is unknown, as subsequent glaciations have obliterated the record (Mellars, 1996).

Pollen and speleothem sequences from a variety of sites in northern, central, and western Europe indicate that open vegetation, with sedges, grasses, and other tundra-based plants, dominated the landscape (Mellars, 1996; van Andel & Tzedakis, 1996; Tzedakis et al., 1997; Müller et al, 2003; Spötl & Mangini, 2006). Northern European summer temperatures have been estimated to be no greater than 8°C (46°F), which is 8-10°C (14.4-18°F) colder than in the Holocene (Mellars, 1996). Central European temperatures were also lower, with an average temperature of -13°C (8.6°F) in the winter, and 14°C (57.2F°) in the summer (Klotz et al., 2004).

Pollen evidence from southern and eastern European sites indicate desert and steppe vegetation, such as *Artemisia* (sagebrush), *Chenopodiaceae* (flowering plants), and *Thalictrum* (flowering plants), with some indication of woodland (Cheddadi & Rossignol-Strick, 1995; Mellars, 1996; van Andel & Tzedakis, 1996; Kukla et al., 2002; Müller et al., 2003; Shackleton et al., 2003; Klotz et al., 2004). Indeed, some localized areas, such as the Iberian Peninsula, preserved patches of hardier trees such as *Pinus* (pine), *Salix* (willow), and *Betula* (birch) (Mellars, 1996; van Andel & Tzedakis, 1996; Kukla et al., 2002; Klotz et al., 2004; Hodge et al., 2008). These refugia would have allowed for faster immigration of interglacial species during warmer intervals (Hodge et al., 2008). Additionally, the reduction in temperatures would not have been as marked as in northern areas, with an annual decrease of 5-6°C (9-10.8°F) (Mellars, 1996).

Sub-stages 5c and 5a are also referred to as St. Germain I and II, respectively, and are recognized as interstadial intervals (Guiot et al., 1993; Tzedakis et al., 1997; Gamble, 1999).

Although the overall ice volume decreased by half of what it was during the stadial intervals, the volume was still greater than what is typically found during full interglacial periods (Mellars, 1996). What is, perhaps, the most interesting aspect of these two interstadials is the diversity of climate and vegetation found throughout Europe (Mellars, 1996).

Northern Scandinavia transitioned from an open tundra climate to one characterized by concentrated birch (*Betula*) and pine (*Pinus*) (Mellars, 1996; van Andel & Tzedakis, 1996; Gamble, 1999). Northern Europe, such as the Netherlands, Denmark, northern Germany, and England, were covered with conifer trees, such as *Pinus* (pine), *Abies* (fir), *Betula* (birch), and *Picea* (spruce) (van Andel & Tzedakis, 1996). Average summer temperatures were lower than those in the Holocene, and predicted to have been approximately 12°C (53.6°F) (Mellars, 1996).

Central Europe was dominated by more warm-loving, deciduous trees, such as *Quercus* (oak), *Corylus* (hazel), and *Carpinus* (hornbeam) (Mellars, 1996; Klotz et al., 2004; Gómez-Orellana et al., 20070). The early re-emergence of these trees signals that localized refugia must have existed north of the Alps during the preceding stadial period (Müller et al., 2003). Summer and winter temperatures are estimated to have been 18-20°C (64.4-68 F) and 2.2°C (36°F), respectively (Mellars, 1996; Klotz et al., 2004). Vegetation south of the Alps was a mixture of deciduous trees and Mediterranean taxa (van Andel & Tzedakis, 1996).

Pollen sequences from northwestern Iberia show a wooded landscape during these times. However, there is a minor difference between 5c and 5a in regards to the percentage of *Fagus* (beech), with 5c having higher pollen counts, and 5a having lower counts and discontinuous sequences (Gómez-Orellana et al., 2007). Mediterranean areas, such as the

Levantine Basin, show pollen sequences with a small quantity of evergreen and deciduous forest, and a more widespread semidesert and desert (Cheddadi & Rossignol-Strick, 1995).

Sub-stages 5c and 5a, although interstadials, never reached the maximum temperature, sea-surface temperatures, sea levels, or continental ice sheet retreat as sub-stage 5e. In fact, there is a pattern within the interstadials of OIS 5 that reflect a gradual decline in climate conditions. However, what began as a slow decline ended abruptly with a period known as the middle glacial period, or OIS 4.

OIS 4 (71-57 kyr)

Oxygen isotope stage 4 is also known as the Pleniglacial, and represents an extremely cold period, with no measurable interstadial sub-stages (Gamble, 1999). Indeed, global sea levels decreased and $\delta^{18}O$ levels increased, signaling an expansion of the global ice volume (Mellars, 1996; van Andel & Tzedakis, 1996; Gamble, 1999; Spötl & Mangini, 2006). Although the ice sheets did not expand as far as the last glacial maximum (LGM) of 18,000 years ago, they did develop further than during sub-stages 5d and 5b (Mellars, 1996; Gamble, 1999). The extent of their development is obscured because their margins have been eroded and buried by the ice advance of the LGM; however, there is some indication, although controversial, that areas of Scandinavia, Poland, and northwest Germany were under ice (van Andel & Tzedakis, 1996).

Vegetation records indicate a general deforestation, with progressive change from north to south (Gómez-Orellana et al., 2007). Polar desert would have occupied the areas just south of the ice sheet, including north-central Poland, north-central Germany, the Netherlands, and Belgium (van Andel & Tzedakis, 1996). The majority of central Europe

was covered by a mosaic of open tundra and cold steppe vegetation, with a few conifer refugia further south (van Andel & Tzedakis, 1996; Müller et al., 2003; Fletcher et al., 2010).

The Iberian Peninsula and southern Europe were dominated by cold, arid steppe vegetation (van Andel & Tzedakis, 1996; Fletcher et al., 2010). Speleothem evidence suggests a decrease in effective precipitation in southeast Spain, supporting an arid climate (Hodge et al., 2008). However, pollen evidence from the northwest Iberian coast shows that this area was dominated by *Erica* (heath), *Calluna* (heather), and Poaceae (true grasses), indicating grassland vegetation (Gómez-Orellana et al., 2007). This climate condition has also been supported by marine pollen cores from the Bay of Biscay (Fletcher et al., 2010). It is suggested that although the northwest Iberian coast was affected by the cold conditions of OIS 4, the humidity from the coast allowed for this type of vegetation to flourish (Gómez-Orellana et al., 2007). Therefore, coastal vegetation and, consequently, climate, may have differed from that of inland areas, providing a more stable environment for Neandertal dietary exploitation (Finlayson, 2008).

Marine pollen sequences from the Mediterranean areas predominantly suggest a treeless, semi-desert climate, with high pollen counts of *Artemisia* (sagebrush) (Cheddadi & Rossignol-Strick, 1995; van Andel & Tzedakis, 1996; Fletcher et al., 2010). Pollen records from the northwest Mediterranean area show high counts of sagebrush; however, the discontinuous and short nature of the core, along with the high percentage of reworked ("recycled") pollen makes interpretation difficult (Fletcher et al., 2010).

Oxygen isotope stage 4 represents a short, but relatively stable glacial period over much of western Eurasia. It was once thought that the subsequent OIS stage continued the cycle into a warm, stable interglacial, but that was not the case. Ice cores from Greenland

first documented a shift from stability during OIS 3, when rapid, oscillating climate conditions were recorded over much of the globe (Dansgaard et al., 1993). For purposes of this dissertation, it is an important period of time; it is during OIS 3 that the Neandertals became extinct, and the anatomically modern humans moved into areas occupied by Neandertals.

OIS 3 (57-25 kyr)

Oxygen isotope stage 3 is also referred to as the Interpleniglacial, and was a period of gradually deteriorating climate conditions with sudden, frequent cold fluctuations (Gamble, 1999). Large icebergs breaking away from glaciers, through either internal forcing (large accumulated mass of the iceberg itself) or external forcing (shifts in solar radiation), is thought to have been the catalyst for such events, known as Heinrich events[9] (van Andel & Tzedakis, 1996). The large icebergs melted, adding copious amounts of cold, fresh water into the North Atlantic, changing ocean temperature, ocean circulation patterns, and, consequently, continental land conditions (van Andel & Tzedakis, 1996; Gamble, 1999)

The most detailed indicator of these quickly changing conditions is found in long ice cores from Greenland, which have recorded a minimum of 12 considerable climate changes (Dansgaard, et al. 1993; Mellars, 1996). These ice cores suggest that Greenland temperatures during the warm periods rapidly rose by 5-8°C (9-14.4°F), allowing global sea levels to rise and $\delta^{18}O$ to lower, sometimes in as little as 50 years (Dansgaard et al., 1993; Mellars, 1996). Most of the warm periods were short, ending within 1,000 years, but there are longer interstadial periods that lasted 2-4,000 years (Mellars, 1996; Gamble, 1999).

[9] Cold and warm oscillations are known as Dansgaard-Oeschger stadials and interstadials, respectively; however, those D/O stadials associated with the icebergs breaking off in the North Atlantic are known as Heinrich events (Dansgaard et al., 1993).

The rapid fluctuations make climate and vegetation interpretations difficult at best, because trees and plants could not recover and migrate north fast enough during warm conditions (Mellars, 1996). The consequence is an underrepresentation of vegetation (Mellars, 1996). Regardless, paleoclimate reconstructions have been produced, usually utilizing a multi-proxy approach.

Pollen sequences from a longer (2-4,000 years) OIS 3 interstadial present a gradient from north to south (van Andel & Tzedakis, 1996; Alfano et al., 2003). Northern Europe, specifically northern Germany, the Netherlands, and the eastern Baltic, would have been covered by a shrub-tundra vegetation of *Betula* (birch), *Salix* (willow), and *Juniperus* (juniper) (van Andel & Tzedakis, 1996; Fletcher et al. 2010). The alpine foreland and eastern France are reconstructed as being covered by open woodland, such as *Pinus* (pine), *Picea* (spruce), and *Betula*; however, warm-loving trees did not migrate north of the Alps (van Andel & Tzedakis, 1996). Pollen records from southwest Germany show high percentages of *Betula*, *Pinus*, and, at times, *Juniperus* (Müller et al., 2003; Fletcher et al. 2010). Precipitation and temperature reconstructions indicate lower precipitation and a lower overall temperature of 4°C (7.2°F) than in the Holocene (van Andel & Tzedakis, 1996).

Iberia, specifically southern Spain, flourished with juniper and pine, along with deciduous oak populations (van Andel & Tzedakis, 1996; d'Errico & Sánchez-Goñi, 2003). Deciduous oak and pine woodland were also recorded in Cataluña, in northeast Spain (van Andel & Tzedakis, 1996). The northwest and central coasts of Iberia provide further evidence of deciduous woodland, with *Quercus* and *Betula* dominating the pollen sequences (Gómez-Orellana et al., 2007; Fletcher et al. 2010).

Central and southern Italy, along with northern Greece, are documented as having deciduous woodland that was open in character; in fact, high tree densities are only recorded in a few areas where soil and precipitation conditions were sufficient for growth (van Andel & Tzedakis, 1996). Taxa present there include *Quercus*, *Corylus*, *Fagus*, and *Ulmus*, while Southern Greece had deciduous and evergreen varieties of *Quercus*, *Pinus*, and *Juniperus* (van Andel & Tzedakis, 1996; Fletcher et al. 2010).

Lastly, the Near East pollen sequences record a steppe or semi-desert environment with patches of evergreen woodland (Cheddadi & Rossignol-Strick, 1995). However, there is some evidence, vis-à-vis mean body size of spur-thighed tortoises, that areas in the Near East, at least at Kebara Cave in Israel, fluctuated between cold/arid and warm/wet conditions (Speth & Tchernov, 2003).

OIS 3 as a factor in Neandertal extinction

Oxygen isotope stage 3 brought pulses of climatic chaos to the western Eurasian landscape. Constantly fluctuating conditions, sometimes within a few hundred years, must have brought adaptive challenges to all species living at the time. In fact, many species of European megafauna, such as *Ursus spelaea* (cave bear), *Mammuthus primigenius* (mammoth), *Elephas antiquus* (straight-tusked elephant), *Coelodonta antiquitatis* (wooly rhino), and *Stephanorhinus kirchbergensis* (Merck's rhino) went extinct during this stage (Stewart et al., 2003). Consequently, researchers have investigated the likelihood of OIS3-based climatic stress as the main factor for Neandertal extinction (d'Errico & Sánchez-Goñi, 2003; Stewart et al., 2003; Stringer et al., 2003; Stewart, 2005).

An interesting approach to this issue is the investigation of changing migratory patterns of both Neandertals and AMH across Europe during OIS 3 (van Andel et al. 2003). Dated sites with clear hominin archaeological indicators (i.e. sites with Mousterian industries are Neandertal, those with Aurignacian lithics are AMH, and those with Gravettian tools are later AMH) were tracked throughout specific timeframes of OIS 3 (van Andel et al. 2003). The Neandertal migratory pattern showed a clear link with climate change; in fact, the data suggest expansions across the Mediterranean and throughout central Europe during longer, stable interstadials, and contractions into coastal areas, such as the Atlantic coast to the west and the Black Sea to the southeast, during climate deteriorations (van Andel et al. 2003; Finlayson, 2008). Indeed, coastal areas in Iberia, Italy, and the Black Sea area make up the late Neandertal site locations of OIS 3 most likely due to their more stable climate conditions and terrestrial and marine resources (Bar-Yosef, 2004; Finlayson, 2008).

Anatomically modern humans, specifically, those sites that have the earlier Aurignacian lithic industries, show a similar constriction pattern to the west and southeast during climate decline (van Andel et al. 2003). Interestingly, later AMH sites, evidenced by Gravettian industries, demonstrate a migration and expansion north of the trans-European mountain ranges, where they actually peaked during the initial descent into the LGM (van Andel et al. 2003).

Both the Neandertals and AMH show similar dispersal patterns in both warm expansions and cold constrictions, with a withdrawal into southern, coastal European areas towards the decline into the LGM (van Andel et al. 2003). However, there is some question whether these patterns are indicative of direct climate impact or indirect impact through vegetation and resource changes (van Andel et al. 2003). It has been suggested that perhaps

the Neandertal and AMH groups were adapted to temperate food resources and were unable to adapt to near-arctic or arctic conditions as were the later AMH (Davies & Gollop, 2003; van Andel et al. 2003; Stewart, 2005).

The inability of Neandertals to adapt to near-arctic or arctic conditions is a surprising hypothesis since, as previously discussed, several characteristics of Neandertal morphology have been described as hyperarctic (Havarti, 2007). However, thermoregulation analyses suggest they would have had a negligible advantage over AMH in lower critical and minimum sustainable temperatures, even when adjusting for increased muscle mass and a dietary-related increase in basal metabolic rate (BMR) (Aiello & Wheeler, 2003). Moreover, deteriorating conditions throughout the second half of OIS 3 would have required cultural buffering in the form of clothing or insulation, and, even if present, the high cost of maintaining homeostasis in the form of internal body heat would have only been possible with sufficient dietary intake (Aiello & Wheeler, 2003).

Another approach to examining the costs of the OIS 3 climate oscillations is examining the Neandertal extinction in relation to other European megafauna that also went extinct at this time. (Stewart et al. 2003; Stewart, 2005). Several Late Pleistocene megafauna, such as those listed previously, went extinct at approximately the same time as Neandertals. Although vertebrate paleontologists disagree as to the reason for the megafauna extinctions (climate-driven versus human overkill), they agree that these species were similar in their large size, long breeding intervals, and small population numbers (Stewart et al. 2003; Stewart, 2005).

An interesting pattern was found when the range of megafauna that existed over the European continent before, during, and after OIS 3 was examined (Stewart et al. 2003).

Extant taxa either maintained their distributions across Europe, or became constricted in one of two areas: the north (or mountainous areas) or east (toward southwest Asia) (Stewart et al. 2003). Those taxa that went extinct did so either at the approach of the LGM (before 18,000 years ago) or at the end of the Pleistocene (approximately 10,000 years ago) (Stewart et al. 2003). Moreover, all the taxa that went extinct at the approach of the LGM, *Elephas antiquus*, *Stephanorhinus kirchbergensis*, and the Neandertals, all show the same decrease in population numbers and western/southwestern migratory withdrawal (Stewart et al. 2003; Stewart, 2005). This may suggest that cold climate and vegetation resource changes could have both played a role in their extinction events (Stewart et al. 2003; Stewart, 2005).

It is interesting to note that the only taxa that increased their numbers through OIS 3 were *Ovibos moschatus* (musk ox) and *Homo sapiens* (Stewart et al. 2003). The modern distribution of *Ovibos moschatus* is in the arctic tundra of northern Scandinavia, Greenland, Alaska, and Canada, and its excellent adaptation to cold may have allowed it to not only survive, but flourish (Stewart et al. 2003). Taken in light with the northern migration and expansion of the Gravettian-producing AMH near the LGM, one might hypothesize that these later hominins were, in fact, better able to adapt to arctic conditions than were the Neandertals.

In spite of this, researchers have also considered cold stages of OIS 3, specifically, certain Heinrich events (H4), as allowing Neandertals to survive as long as they did (d'Errico & Sánchez-Goñi, 2003). The Iberian Peninsula is often recognized as one of the last areas of Neandertal survival during OIS 3. The cold periods, as with the interstadials, brought a heterogeneous vegetation pattern to the landscape, with the north covered in grassland and the south dominated by desert-steppe (d'Errico & Sánchez-Goñi, 2003). It is argued that the

AMH were only able to live in the northern grasslands during cold pulses because they were unable to adapt to an arid landscape with limited vegetation and fauna (d'Errico & Sánchez-Goñi, 2003). Although Neandertal populations most likely declined as a result of moving to the arid south, they were not in direct competition with the AMH for resources (d'Errico & Sánchez-Goñi, 2003). Therefore, it is not until the end of the Heinrich event that AMH were able to colonize the south and outcompete the Neandertals, driving them to extinction (d'Errico & Sánchez-Goñi, 2003).

The radically changing climate of OIS 3 has long been considered a factor in Neandertal extinction, with the arrival of allegedly behaviorally and cognitively advanced anatomically modern humans taking a principal or secondary role (Svoboda, 2005). However, the fossil and paleoclimate records are fragmentary and discontinuous, with geological processes and dating methods posing challenges to those who attempt to tease information from them.

The extinction of the Neandertals is most likely a multifaceted phenomenon, with climate, vegetation resource, and animal migratory pattern changes, along with the possibility of direct or indirect competition from modern humans as probable scenarios. Moreover, there might be unexplored factors still awaiting scrutiny and analysis. The investigation of dietary and behavioral strategies of Neandertals, along with those of AMH, is important for uncovering possible differences or similarities between these two hominins, and using an integrative context may help us better understand motive forces behind the extinction of the Neandertals.

Dietary & Behavioral Reconstructions of Neandertals

Several indirect and direct lines of evidence have been utilized to reconstruct the dietary and behavioral strategies of Neandertals. Indirect methods include morphology and lithic and faunal assemblages, whereas direct techniques incorporate stable isotope as well as microwear analyses. These approaches have all benefited fossil hominin research generally, and Neandertal studies specifically; however, some techniques pose more complex challenges than others.

For example, skeletal and dental morphologies have long been used as evidence that Neandertals were adapted to cold conditions, with some researchers even referring to these hominins as hyperarctic (Havarti, 2007). However, thermoregulation research has shown that Neandertals would have had a negligible advantage over AMH in cold climates, even with cultural buffering (Aiello & Wheeler, 2003). Moreover, paleoanthropologists disagree as to the relatedness of Neandertals and AMH; those who support a direct line apply Bergmann's and Allen's Rules to evaluate Neandertal robusticity with AMH gracility, but if they are separate species, these rules cannot be applied and morphological comparisons between the two hominins cannot be made (Aiello & Wheeler, 2003; Stewart, 2005).

However, it is recognized that morphological characteristics are an important and productive avenue to pursue. Therefore, the discussions of indirect and direct evidence will include morphology, lithic and faunal assemblages, and stable isotope and dental microwear analyses, respectively. These proxies represent the major contributors of Neandertal dietary and behavioral reconstruction.

Indirect evidence: morphology

Neandertal cranial-dental morphology, as mentioned above, has often been used as phylogeny indicators, although challenges have been presented relating to parallel and convergent evolution, as well as epigenetic factors (Harvati & Weaver, 2006). However, morphological traits have also been used to gain a better understanding of dietary and behavioral adaptations of these hominins. These traits include cheek teeth , incisors, and root morphology (Ungar et al., 1997; Bailey, 2002; Le Cabec et al., 2009; 2010; Kupczik & Dean, 2008; Kupczik & Hublin, 2010).

For example, Bailey (2002) examined Neandertal post-canine dentition and scored them using the ASUDAS scale, a standardized system developed for scoring modern human variation in both tooth crown and root morphology, but which has been expanded to fossil hominins. While it was generally acknowledged that Neandertal incisor morphology was unique, the post-canine dentition was regarded as similar to that of modern humans (F. Smith, 1976). However, Bailey (2002) found differences, including a more complex mandibular premolar occlusal morphology in Neandertals that included lingual cusps and continuous transverse crests. Neandertal mandibular molars also had different morphology, which included additional occlusal fissures and crests, including a mid-trigonid crest, elongated roots, and enlarged pulp chambers (Bailey, 2002; Kupczik & Hublin, 2010).

While the crown morphology has been described as phylogenetically significant, the uniquely elongated root and enlarged pulp chamber morphology, often referred to taurodontism, has been described as advantageous to tooth function (Kupczik & Hublin, 2010). One hypothesis suggested the large pulp cavity allows for secondary dentine to be deposited on pulp walls in response to heavy occlusal wear (Coon, 1962; Blumberg et al.,

1971; Hillson, 1996). Another idea put forth proposed that the position of the elongated root, specifically, the bifurcation or trifurcation areas of the mandibular and maxillary molars, respectively, provides protection of this area from the oral cavity and, consequently, periodontal disease (Blumberg et al., 1971).

A third line of research suggested that root attachment area is correlated with occlusal loads and mechanical properties of foods in primates (Kupczik & Dean, 2008). That is, hard-object feeding primates had greater root surface areas than those taxa that ate mechanically less challenging foods (Kupczik & Dean, 2008). In a study examining differences in molar root surface areas for Neandertals, Aterian *Homo sapiens*, and recent *Homo sapiens*, Neandertals exhibited similar root surface areas for both their mandibular first and second molars (Kupczik & Hublin, 2010). This suggested that muscle force was nearly equal for both mandibular molars in Neandertals, whereas the muscle force peaked at the M_2 and M_1 of the Aterian *Homo sapiens* and recent *Homo sapiens*, respectively (Kupczik & Hublin, 2010). The large root surface areas for both mandibular M_1's and M_2's in Neandertals may indicate an adaptation to processing large, mechanically demanding food items (Kupczik & Hublin, 2010).

Analyses have also been completed for incisor roots to gain better understanding of Neandertal anterior tooth loading regimes (Le Cabec et al., 2009; 2010). Previous analyses determined that Neandertal incisor roots were longer than those for *Homo sapiens* (Le Cabec et al., 2009). Additional, expanded research confirmed that Neandertal maxillary central and lateral incisor roots were not only signficantly longer than *Homo sapiens*, but also had more volume, greater surface area, and larger labial-lingual and mesial-distal diameters (Le Cabec

et al., 2009, Le Cabec, personal communication). These data suggest Neandertals may have participated in different anterior loading regimes than *Homo sapiens* (Le Cabec et al., 2009).

Similar research focused on Neandertal incisor beveling patterns, and their relationship to non-dietary and dietary causes (Ungar et al., 1997). The beveling angle, defined as the angle between the labial and incisal surfaces, of Neandertal and recent *Homo sapiens* maxillary and mandibular central incisors were examined and recorded. Changes within beveling angles within each modern human comparative group (Ipiutak from Point Hope and Puebloans from New Mexico) allowed for wear sequence patterns to be generated for each sample. These wear patterns were then compared to the Neandertal beveling patterns. Differences in beveling angles decreased from Neandertals to the Ipiutak to the Puebloan samples, suggesting differences in the degree of beveling and not the pattern of it (Ungar et al., 1997). This progressive decrease in angles was interpreted to indicate differences in incisor procumbancy, interproximal wear that may have allowed for "posterior tipping" of the maxillary incisors, or separation of maxillary and mandibular incisal edge surfaces during edge-to-edge bite (Ungar et al., 1997).

Indirect evidence: techniques, models, and theoretical frameworks of lithic and faunal assemblages

The two indirect lines of evidence used most often in Neandertal dietary and behavioral reconstruction are associated lithic and faunal assemblages, and reconstructions have been completed on several areas where Neandertals have been found, including the Near East (Lieberman & Shea, 1994; Shea, 1998, 2003), the Caucasus Mountains (Hoffecker & Cleghorn, 2000; Adler et al. 2006), Croatia (Karavanić and Smith, 1998, 2000; Paunovic,

2003; Ahern et al. 2004; Miracle, 2005); Poland (Wojtal & Patou-Mathis, 2003; Patou-Mathis, 2004), Germany (Conard & Prindiville, 2000; Krönneck et al., 2004; Münzel & Conard, 2004), Italy (Fiore et al., 2004; Valensi & Psathi, 2004), France (Boyle, 2000; Valensi, 2000; Hardy, 2004; Steele, 2004; Valensi & Psathi, 2004), Spain (Vaquero et al. 2001; Steele, 2004), Portugal (Antunes, 2000a, 2000b, 2000c; Antunes et al. 2000; Raposo & Cardoso, 2000), and Gibraltar (Stringer et al. 2008). Many of these studies use both indirect indicators, so lithic and faunal assemblages will be discussed simultaneously; however, a brief review of the techniques and theoretical frameworks behind the research will be discussed first.

The Mousterian lithic techno-complex is most often associated with Neandertals, although early Upper Paleolithic Neandertal sites from northern Spain and parts of France contain a different lithic industry, known as the Châtelperronian (Hublin et al. 1996; Zilhão, 2006; Zilhão et al. 2006). Studies of Mousterian assemblages have predominantly relied on Bordesian typologies, a classification technique developed by François Bordes that emphasizes the presence of retouched tools such as sidescrapers (*racloirs*), points, backed knives, and notched, denticulated, and bifacial tools (Bordes, 1961, 1968; Mellars, 1996; Clark, 2002).

Bordes recognized four different Mousterian types through time and space, known as facies, based on morphological characteristics (Bordes, 1961, 1968). He referred to the four types as Denticulate, Typical, Mousterian of the Acheulean Tradition, and Charentian (with Ferrassie and Quina as subgroups), providing an important means for the organization and comparison of Neandertal lithics from countless sites; however, several problems have arisen with the technique (Freeman, 1992).

First, researchers found significant variation between sites, suggesting the four facies were not sufficient to describe the unique attributes of some remains (Clark, 2002). Second, others suggested that a system based on functional, rather than morphological characteristics, would be more appropriate (Binford, 1968). Lastly, some paleoanthropologists criticized the system, stressing an inherent bias between producer, material culture, and behavior (Clark, 2002). More specifically, there were two underlying assumptions in the typologies between Mousterian and Aurignacian tools. The first was that production sequences, modes of retouching, and configurations could be interpreted as forms of social learning and cognitive ability (Clark, 2002). In other words, the more complex and diversified the lithic industry, the more advanced the brain. The second assumption is closely linked with the first in that differences between Neandertal and AMH lithic industries accurately reflect differences in their diet, behavior, and overall skill (Clark, 2002).

Differences in skill, especially as they relate to modes of diet and behavior, are clearly seen in debates surrounding Neandertal faunal exploitation. Faunal exploitation, the method in which animals were obtained and utilized, is directly associated with hominin diet insofar as how they made use of meat and fat resources, as well as other aspects of behavior, such as technology development, mobility, and social organization (Marean & Assefa, 1999). For example, tactical hunting techniques, such as whaling on the arctic coast, require cooperation and reciprocity among hunters, whereas single-animal encounter strategies do not (Marean & Assefa, 1999). Therefore, determining the hunting skills and strategies of fossil hominins through both lithic and faunal assemblages can help us understand their behavioral repertoire.

There are three primary datasets that paleoanthropologists use when examining and interpreting a faunal assemblage. The first is skeletal element counts, which is related to levels of nutrition; that is, different skeletal elements are associated with different amounts of nutritional quality and quantity, and therefore, are ranked by levels of nutritional preference (Marean & Assefa, 1999; Rabinovich & Hovers, 2004). The first preferred resource is flesh, the second is bone marrow, and the last is bone grease found in cancellous bone throughout the body (Marean & Assefa, 1999). The premise is that primary consumers (i.e. hunters) will select the top-ranking areas first, whereas the secondary consumers (i.e. scavengers) will only have the lower level preferences from which to select (Marean & Assefa, 1999). If Neandertals were hunters, it would be reflected in their faunal assemblages as a high incidence of flesh-bearing bones. On the other hand, if they scavenged, bones with little to no flesh will be represented the most.

The second dataset is bone modification, such as lithic tool or carnivore tooth marks. Lithic tool marks on faunal bones provide evidence of direct contact between the bone and hominins, and, depending on the pattern of marks or breakage, can indicate disarticulation and dismemberment, flesh removal, or periosteum removal for marrow procurement (Marean & Assefa, 1999; Rabinovich & Hovers, 2004). From these patterns, researchers can hypothesize hominin subsistence behavior as it relates to meat resources. For example, marks on flesh-heavy bones would suggest the hominin was the primary consumer, whereas periosteum-removal marks or breakage patterns might indicate the hominin was scavenging (Marean & Assefa, 1999). Challenges exist, however, because many patterns can overlap in behavioral interpretations, so it is helpful to examine the carnivore tooth marks as well. Carnivore tooth marks can signify an animal's involvement in creating (as the hunter) or

scavenging the assemblage, and have also been used to suggest scavenging by hominins after the carnivore was finished (Marean & Assefa, 1999).

The third common dataset is mortality profiles, which examines the representation of animal age-at-death. While some mortality profiles have a high incidence of young and old individuals, others show prime-age or a combination of young, prime, and old animals (Marean & Assefa, 1999; Rabinovich & Hovers, 2004). Although there are several difficulties in using mortality profiles, such as little ethnographic data correlating them with hunting and transport strategies, some suggest that assemblages high in prime-age animals represent hunting, not scavenging tactics (Marean & Assefa, 1999; Rabinovich & Hovers, 2004).

These common datasets have been used to propose several different models for Neandertal and AMH faunal exploitation, all of which differ in their predicted amount of scavenging or hunting. At one end of the spectrum is the obligate scavenger model, which describes Neandertals of OIS 6 as predominantly using scavenging strategies to acquire meat resources, with an increased emphasis on hunting medium-sized animals through time (Binford, 1991). Although hunting tactics intensified temporally, large-sized animals were still frequently scavenged (Binford, 1991). This model originated from Binford's work at several French Neandertal sites, as well as the AMH site at Klasies River Mouth in South Africa.

A more moderate framework is the flexible hunter-scavenger model, developed from research at several Neandertal cave sites in coastal Italy (Stiner, 1994). It proposes that Neandertals were not obligate scavengers, but instead, only scavenged when plant foods were available; however, when vegetation resources were no longer accessible, they would

primarily hunt (Stiner, 1994). This model suggests that Neandertals were capable of subsistence strategies that fluctuated between hunting and scavenging in tandem with food resource availability that changed with climate (Stiner, 1994).

A third, more hunting-based concept is called the less-adept hunter model, and derives its data from several Middle and Late Stone Age sites in Africa (Klein & Cruz-Uribe, 1996). This model suggests that Middle Stone Age hominins were hunters, but were not as effective at hunting as modern humans (Klein & Cruz-Uribe, 1996). This difference is suggested to be due to a brain change that resulted in improved social and technological skills, allowing for more effective hunting (Klein & Cruz-Uribe, 1996).

At the other end of the spectrum is the fully adept hunter model, which was developed from several Neandertal sites, including some of the same that Binford examined to propose his obligate scavenger model (Chase, 1986, 1988). This idea stemmed from the reinterpretation of Binford's datasets, and the suggestion that the faunal assemblages appeared to be indicative of only scavenging because the hominins were taking the high-utility parts to other locations (Chase, 1988). The main point of this model is that faunal assemblages must be interpreted in light of not only the sample itself, but the context of the site (Chase, 1988).

These datasets and models provide paleoanthropologists and zooarchaeologists with workable frameworks regarding dietary and behavioral strategies of hominins; however, several researchers have found flaws with these techniques. First, taphonomic processes, such as geologic processes and carnivore activities, have seldom been incorporated into interpretive models. Second, and perhaps more importantly, rarely were diaphyses counted in skeletal element analyses or subjected to refitting with epiphyses. This could have

contributed to a misinterpretation of the assemblage itself. As a result, recent interpretations have combined lithic and faunal assemblage datasets to control for these flaws as best as possible, and modern research has spanned the spatial and temporal occupation of Neandertals.

Indirect evidence for dietary and behavioral strategies across Neandertal environs

The Levant

The Levant provides an interesting cultural and social intersection for Neandertals and AMH, since several cave sites in the area were home to both hominins. Specifically, Neandertals have been excavated at Tabūn, Amud, and Kebara Caves, while AMH have been found at nearby Skhūl and Qafzeh Caves (Lieberman & Shea, 1994; Shea, 2003). Moreover, thermoluminescence and electron spin resonance dates indicate the AMH were in the area much earlier than the Neandertals, refuting the popular evolutionary transition from Neandertal to AMH (Shea, 2003).

Although Neandertals and AMH are most often associated with Mousterian and Aurignacian tools respectively, the Levant demonstrates a different pattern, with both hominins utilizing the same lithic techno-complex, often referred to as the Levantine Mousterian (Lieberman & Shea, 1994, Shea, 1998, 2003). The Levantine Mousterian lithic assemblages and their associated hominin fossils mostly date between OIS 6 through 4 (Lieberman & Shea, 1994; Shea, 2003). There are three generally recognized temporal variants, and they are characterized by different frequencies of debitage, blades, few retouched tools, and Levallois points (Lieberman & Shea, 1994; Shea, 1998, 2003). They are usually made of local flint, show evidence of hafting, and microwear analyses have shown

they were used for a variety of purposes, including butchery, hide scraping, and woodworking (Lieberman & Shea, 1994; Shea, 1998).

The faunal assemblages are dominated by medium-to-large animals, such as *Cervus elephas* (red deer), *Gazella gazella* (gazelle), *Dama mesopotamica* (fallow deer), *Capra aegagrus* (wild goat), *Capra ibex* (ibex), *Bos primigenius* (aurochs), *Sus scrofa* (wild boar), *Capreolus capreolus* (roe deer), and equids (Lieberman & Shea, 1994; Shea, 1998, 2003; Rabinovich & Hovers, 2004). Smaller fauna, such as hyrax, tortoise, fox, and hare are also present (Lieberman & Shea, 1994; Shea, 1998; Speth & Tchernov, 2003; Rabinovich & Hovers, 2004). Although larger herbivores, such as *Elaphus maximus* (elephant), *Dicerorhinus mercki* (Merck's rhino), and *Hippopotamus amphibius* (hippopotamus) lived in the area, they are infrequent in faunal assemblages, most likely because of the danger involved in hunting them (Shea, 1998; Rabinovich & Hovers, 2004).

Although these sites show similar types of lithic and faunal assemblages, the frequencies of the tools and animals differ, and, accordingly, behavioral similarity cannot be assumed. Therefore, examining the formation processes of the assemblages can help to discern behavioral differences between the two hominins.

A novel approach to faunal assemblage analyses was used by Lieberman & Shea (1994). They investigated acellular and cellular cementum bands of ungulate teeth (predominantly *Gazella gazella*), which have been demonstrated to reflect season of death and age at death, respectively (Lieberman & Shea, 1994). They found that 52% of the gazelles and other ungulates were hunted during the dry season, and 48% were hunted in the wet season at Kebara. This pattern reflects a multi-seasonal occupation of the Neandertals at Kebara Cave (Lieberman & Shea, 1994). On the other hand, the pattern at Qafzeh indicated

single-seasonal hunting for AMH, as all the gazelles and other ungulates were killed during the dry season (Lieberman & Shea, 1994).

To further justify their argument, they examined the stone tool assemblages and applied lithic microwear analyses. They found that Kebara had a higher frequency of points than Qafzeh. Moreover, microwear analyses of the Kebara points found in the same stratum layer as the ungulates demonstrate a higher percentage of impact-damaged points than those from the Qafzeh ungulate layer (Lieberman & Shea, 1994). This suggests an intensified hunting strategy by the Neandertals.

The combination of the faunal and lithic assemblage data suggests that Neandertals, at least at Kebara, were participating in radiating mobility strategies in which a multi-seasonal, more permanent base camp was established, and less-permanent, highly seasonal sites were used for specialized activities or resources (Lieberman & Shea, 1994; Shea, 2003). Conversely, the faunal and lithic evidences from Qafzeh suggest the AMH there were employing a circulating mobility strategy, whereby a group moves from one temporary base camp to another in a seasonal round (Lieberman & Shea, 1994; Shea, 2003).

When the examination of point frequencies was expanded to the entire Levant area and combined with vegetation reconstruction, more detailed inferences were made. The two different eco-zones found in the Levant, woodland and steppe, varied in their vegetation and animal density. While the woodland had very dense vegetation, and the animals that lived there were solitary or lived in small herds, steppe vegetation was less dense, with large, gregarious species (Shea, 1998). Shea (1998, 2003) hypothesized that efficient woodland hunting strategies would have been encounter hunting, in which hominins would only hunt those animals they encountered first. Less dense steppe vegetation would have required

intercept (ambush) hunting strategies, in which large-grouped species of known location were specifically sought out (Shea, 1998, 2003).

The type and number of tools associated with these two hunting strategies would have differed. Woodland encounter hunting would have required an easily maintained, all-purpose tool, most likely a pointed, wooden spear, which would have allowed for several different types of animals to be taken (Shea, 1998, 2003). Conversely, intercept hunting would have needed reliable tools that would have delivered a severely crippling or lethal wound, such as hafted stone tools (Shea, 1998, 2003). Accordingly, those hominins with high point percentages were most likely using intercept hunting, whereas those with lower percentages were probably using encounter hunting techniques.

When point percentages from several sites in the Levant area, including Qafzeh, Skhul, Kebara, Tabun, and Amud, were considered, along with the two eco-zones found during occupation, an opposing pattern in hunting strategies emerged between Neandertals and AMH (Shea, 1998, 2003). Neandertal sites had much higher percentages of points than AMH, suggesting Neandertals emphasized more steppe-based intercept hunting techniques, whereas AMH used woodland encounter hunting (Shea, 1998, 2003).

Most ethnographic data from modern hunter-gatherer populations reflect flexibility between encounter and intercept hunting, and this flexibility is also inferred for both hominin groups (Shea, 1998). However, an emphasized reliance on meat consumption is suggested for the Neandertals, who appear to have preferred vegetation-lacking steppe environments (Shea, 1998). On the other hand, AMH seem to have preferred woodland environments, which would have contained more plant resources (Shea, 1998, 2003).

Although a decreased emphasis on plants is suggested for Neandertals in the Levant, phytolith assemblages from Amud cave provide evidence to the contrary (Madella et al. 2002). Phytoliths, opal silica bodies that naturally appear in plants to provide structure, support, and defense from consumers, are resistant to decay and can preserve in archaeological contexts (Piperno, 1988). Madella et al. (2002) determined that the Amud Cave phytoliths were not only intact, relatively undamaged, and abundant, but also were equally representative of woody and grass plants.

There were three different types of woody-plant phytoliths, including those found in wood and leaves. Those found in wood, coupled with excavated hearths, suggest Neandertals were using the wood as fuel for fire, which coincides with ash, burned bone, and burned lithic analyses (Madella et al. 2002). The other two phytolith types corresponded to palm leaves and fig trees, which indicate the use of these plant resources in a variety of purposes, including shelter, fuel, fruit, and containers (Madella et al. 2002).

The grass phytoliths suggested a wider exploitation of herbaceous plants by the Amud Neandertals. Phytoliths typical of grassy leaves and stems were abundant throughout the sequences, and suggest that this resource was used for non-dietary purposes, such as bedding and fuel (Madella et al. 2002). The other phytolith type, found in husks of cereal grains, was also found in abundance. This was proposed to be indicative of the Amud Neandertals purposefully collecting mature, seed-bearing grasses, and provided evidence for seed exploitation by these hominins (Madella et al. 2002). This is an extraordinary find, as the authors suggested that Neandertals were participating in seed collection, albeit not as extensively as later modern humans (Madella et al. 2002).

Caucasus Mountains

Differences or similarities in hunting strategies between Neandertals and AMH have also been examined in the Caucasus Mountains area (Hoffecker & Cleghorn, 2000; Adler et al. 2006). Ortvale Klde, a rockshelter located in the southern Caucasus Mountains in the Republic of Georgia, has yielded late Middle and Upper Paleolithic faunal and lithic assemblages (OIS 3-2), and provides a unique opportunity for reconstructing mobility and land-use patterns of these two hominins (Adler et al. 2006).

Skeletal element counts for both Middle and Upper Paleolithic layers were comprised mostly of *Capra caucasica* (mountain tur or goat), with minimal numbers of *Bison priscus* (steppe bison), *Cervus elaphus* (red deer), and *Capreolus capreolus* (roe deer) (Adler et al. 2006). Mortality profiles of the mountain tur remains indicate prime-age adults were favored over young or old individuals (Adler et al. 2006). These data suggest that both hominins were participating in seasonal, selective, intercept hunting of prime-aged mountain tur, establishing not only the value of this resource through time, but also the equivalency of Neandertal and AMH hunting strategies (Adler et al. 2006).

While the faunal data present a uniform hunting strategy between the two hominins, the lithic assemblage demonstrated an important difference. The stratigraphic sequence at Ortvale Klde showed clear Mousterian and Upper Paleolithic layers, with a temporal break between the two archaeological traditions (Adler et al. 2006). While the majority of both lithic assemblages were made of local, high-quality flint, the quantity of non-local obsidian was different (Adler et al. 2006). The obsidian in the Mousterian layers was heavily retouched, and made up only 0.4% of the assemblage; however, obsidian from the Upper

Paleolithic layers was represented by all forms of tool production sequences (i.e. cores, debitage, etc.), and comprised approximately 5% of the total assemblage (Adler et al. 2006).

The nearest obsidian source is over 100 kilometers (62 miles) from the site, and although there is evidence that Neandertals used this resource, the low frequency and heavy retouching suggests they did not travel to or trade with that area often (Adler et al. 2006). Conversely, the increased predominance of obsidian in the Upper Paleolithic layers points to a larger mobility territory or an increased social trading network of modern humans (Adler et al. 2006).

Several Neandertal sites of varying elevations in the northwest Caucasus Mountains provide a unique and expanded perspective of hunting strategies during OIS 4-3 (Hoffecker & Cleghorn, 2000). The lowest elevation sites, Il'skaya I and II, are dual, open-air areas approximately 100 meters (328 feet) above sea level, and are archaeologically represented by all stages of lithic tool production, including cores and sidescrapers (Hoffecker & Cleghorn, 2000). Faunal assemblages were dominated by prime-age *Bison priscus* (steppe bison), with deer and horse species also present (Hoffecker & Cleghorn, 2000). Matuzka Cave, located 720 meters (2300 feet) above sea level, showed a different pattern. The archaeological assemblage was scant, with Mousterian tools representing 50% of the small assemblage, and *Ursus deningeri kudarensis* (cave bear) characterizing 86% of the total faunal remains (Hoffecker & Cleghorn, 2000). However, the authors suggest the cave bear remains were most likely not accumulated by Neandertals, but rather, that the carnivores died during hibernation at times when hominins were absent. Overall, the patterns at Matuzka Cave suggest a limited-activity site (Hoffecker & Cleghorn, 2000).

The remaining three sites evince different faunal patterns than those at lower elevations. Two Borisovskoe Gorge sites, Monasheskaya and Barakaevskaya Caves, are situated at approximately 850 meters (2800 feet) above sea level, and the extensive Mousterian lithic evidence includes cores, debitage, sidescrapers, points, endscrapers, and denticulates (Hoffecker & Cleghorn, 2000). However, the faunal assemblages are much more diversified that those at lower elevations, including subadult and prime-age adult remains of bison, sheep, goat, deer, and horse[10] (Hoffecker & Cleghorn, 2000). Lastly, Mezmaiskaya Cave, situated at 1310 meters (4300 feet) above sea level, has a moderately sized assemblage of Mousterian cores, debitage, and retouched tools (Hoffecker & Cleghorn, 2000). The mammal remains emphasize steppe bison, sheep, and goat, but red deer, cave bear, and marmot (large ground squirrels) are also represented; however, carnivore tooth marks are present on 5-10% of the bovid bones, suggesting some taphonomic damage.

Overall, the pattern of Neandertal occupation in the northwestern Caucasus demonstrates differences in archaeological and faunal preferences, with some sites showing more intensified use than others (Hoffecker & Cleghorn, 2000). Specifically, the pattern reflects a seasonal mobility strategy, with planned and predicted intercept hunting of particular species, although variation does exist in what species was preferred (Hoffecker & Cleghorn, 2000).

Croatia

Several Middle and Upper Paleolithic sites are found in Croatia, and the Dinarid Mountains (Dinaric Alps) roughly divide them into two geographic and climatic zones (Karavanić, 2004). The northwestern sites, such as Krapina, Vindija, Velika Pećina, and

[10] Species names are not provided in the paper.

Veternica, are all cave sites near the capital of Zagreb, whereas the southern, more coastal sites, such as Veli Rat, Ražanac, Ljubač, and Mujina Pećina, are either caves and open-air (Karavanić, 2004). The northwestern sites, especially Krapina and Vindija, are more prominent in paleoanthropology since human fossil remains have been located there, and only Mousterian lithic assemblages have been found at the coastal sites (Karavanić, 2004).

The Krapina lithic and faunal assemblages continue in a similar pattern as other areas discussed. Particularly, the lithic assemblages are clearly Mousterian, with the nearby river cobbles providing the most exploited resource for tool production (Simek & Smith, 1997; Karavanić, 2004). The most common tool type is the sidescraper, which constitutes over half of the total assemblage, but notched, denticulate, and backed knives are also present (Simek & Smith, 1997; Karavanić, 2004). The majority of the tools were made from volcanic and silicified tuff, but chert was also used frequently (Simek & Smith, 1997; Karavanić, 2004). Faunal remains consisted mostly of *Bos* (bison), *Ursus spelaeus* (cave bear), and *Castor fiber* (beaver), with the presence of cave bear suggestive of carnivore denning and a sporadic occupation by Neandertals (Karavanić, 2004).

Krapina is a significant Neandertal site because of the number of fossil remains that have been excavated there. While the fossils allow for in-depth investigation into morphological traits, they also hint at behavior. Specifically, researchers have postulated cannibalism due to bone breakage and burning patterns, along with cut marks indicative of defleshing and disarticulation; however, this interpretation is controversial, and other explanations, such as primary or secondary burial practices have been proposed (Trinkaus, 1985; Russell, 1987; White, 2001).

Vindija Cave is also significant in paleoanthropology, but not due to claims of cannibalism. Instead, this site shows both Neandertal and AMH fossils and artifacts, allowing some to suggest Vindija is a prime example of biocultural transition (Karavanić & Smith, 1998, 2000; Ahern et al. 2004). The earlier stratigraphic levels at Vindija have yielded Mousterian artifacts, made from locally available white quartz, and associated Neandertal fossils; however, it is the Late Mousterian levels, G3-G1, that are important for interpretations of the Middle to Upper Paleolithic transition (Karavanić & Smith, 1998; Ahern et al. 2004).

The G3 level, dated to approximately 42,000 years BP, demonstrates Neandertal fossil material with Mousterian tools (Karavanić, 2004). The majority of the lithic assemblage from this layer is made from white quartz, and consists of various types of sidescrapers, denticulates, and backed knives (Karavanić & Smith, 1998). The presence of some Upper Paleolithic tools, such as endscrapers and blades, are also recorded, but could have gotten there by cryoturbation (frost churning) in the cave (Karavanić & Smith, 1998). The G2 level also shows Mousterian tools made of white quartz; however, this level is small, and is not present in all parts of the cave, making layers G3 and G1 continuous in many areas (Karavanić & Smith, 1998).

The G1 layer was the most unusual, as it contained Neandertal fossils with both Mousterian and Upper Paleolithic tools (Karavanić & Smith, 1998, 2000; Ahern et al. 2004). The typical Mousterian lithics were present, such as various types of sidescrapers and denticulates, but were predominantly made of chert. (Karavanić & Smith, 1998; Ahern et al. 2004). The Upper Paleolithic tools included an Aurignacian blade and bone implements,

including points, a decorated bear baculum, and a bone button Karavanić & Smith, 1998, 2000; Ahern et al. 2004).

The pattern found between layers G3-G1 suggested possible interaction between Neandertals and AMH. Specifically, the change in commonly used lithic raw material, from white quartz to chert, along with the Neandertal remains associated with bone tools in the G1 layer, may indicate imitation of or trade with modern humans (Karavanić & Smith, 1998, 2000; Ahern et al. 2004). However, this has been contested, as cryoturbation and bioturbation occur in other areas of the cave, and may account for the mixing of archaeological materials (d'Errico et al., 1998).

The open-air, coastal sites yielded only Mousterian lithic assemblages that were predominantly denticulated and notched tools made from local, low-quality chert and flint (Karavanić, 2004). The Late Mousterian (OIS 3) cave site in this area, Mujina Pećina, produced Mousterian lithic assemblages with retouched flakes, notched, and denticulated pieces made from locally available chert (Karavanić, 2004). Mujina Pećina also had evidence of fire, with charcoal analyses indicating *Juniperus* was used for fuel (Karavanić, 2004).

The faunal assemblages at Mujina Pećina changed though time, with red deer, chamois (goat-antelope species), and ibex dominating colder periods and wild goat dominating warmer intervals (Karavanić, 2004; Miracle, 2005). Although evidence for cave bear scavenging was found in both cold- and warm-climate assemblages, bears were only able to access the cave for habitation purposes during warm periods (Miracle, 2005). Therefore, the faunal and taphonomic data together suggested the Neandertals at Mujina

Pećina were not only competent hunters, but also controlled access to the cave during colder conditions when competition for shelter would have been high (Miracle, 2005).

Poland

There are limited data from the Middle Paleolithic sites in Poland, due to the recovery of few artifacts and taphonomic damage; however, information about Neandertal subsistence behaviors can still be teased from the data at hand. Both cave and open-air sites have been investigated in Poland, and the majority of them are located in the Kraków-Częstochowa upland in the south-central part of the country (Wojtal & Patou-Mathis, 2003).

Cave sites include Ciemna, Raj, Nietoperzowa, Deszczowa, and Dziadowa Skala caves (Wojtal & Patou-Mathis, 2003). All of these sites have yielded some Mousterian tools, most often sidescrapers made of local flint, although some flint was from resources over 50 kilometers (31 miles) away (Wojtal & Patou-Mathis, 2003; Patou-Mathis, 2004). The faunal assemblages have been affected heavily by carnivore damage, as indicated by gnaw marks on the bones (Wojtal & Patou-Mathis, 2003). Accordingly, these cave sites are dominated by *Ursus spelaeus* (cave bear), and other carnivores, such as wolf, polar fox, hyena, and cave lion (Wojtal & Patou-Mathis, 2003; Patou-Mathis, 2004). The dominance of carnivores in the faunal assemblages, along with few burned or cut-marked remains of large herbivores, such as reindeer, red deer, and roe deer, suggest that Neandertals only used these sites as temporary, short-term shelters (Wojtal & Patou-Mathis, 2003; Patou-Mathis, 2004).

Moreover, there are some interesting inferences that can be drawn from the cave faunal assemblages. For example, Ciemna Cave had evidence of *Capra* spp., which provided the first indication of wild goat in Pleistocene Poland (Wojtal & Patou-Mathis, 2003). Raj Cave assemblages, dating to OIS 3, showed differences during interstadial and

stadial intervals (Patou-Mathis, 2004). The interstadial layer contained the same MNI (minimum number of individuals) for both large herbivores and carnivores, with eight reindeer, horse, bison, and red deer individuals making up the herbivore sample, and eight cave bear, wolf, hyena, and lion remains comprising the carnivore sample (Patou-Mathis, 2004). The stadial layer contained three times the number of large herbivores, with horse, reindeer, bison, mammoth, red deer, wooly rhinoceros, and moose represented (Patou-Mathis, 2004). The carnivore assemblage was nearly double that of the interstadial layer, with 14 MNI consisting of cave bear, wolf, red and arctic fox, hyena, and lion (Patou-Mathis, 2004). The difference in remains between the two layers was suggested to indicate a shorter presence or fewer Neandertal individuals at the site during the warm period; however, taphonomic processes, such as fragmentation and water percolation, have affected the bones, especially in the interstadial layer (Patou-Mathis, 2004).

It should be noted that few clear indications of cut marks were present in either layer, although the mortality profiles from the stadial layer suggested prime-age horse and reindeer hunting (Patou-Mathis, 2004). It is also interesting to note that charcoal analysis indicated *Pinus sylvestris* (Scots Pine) was used extensively for fuel during the interstadial layer, and a reduction in charcoal during the stadial interval coincided with a decrease in forest and an increase in arid conditions (Patou-Mathis, 2004).

There are few open-air sites with faunal assemblages in Poland, but Zwolen and Skaratki are two that have provided interesting data. Dating to OIS 4, Zwolen assemblages indicated that horse was the preferred food source, comprising 60% of the total collection (Wojtal & Patou-Mathis, 2003). Other large mammals, such as mammoth, rhinoceros, and reindeer were also recovered (Wojtal & Patou-Mathis, 2003). The skeletal element profiles

at Zwolen indicated this may have been a kill & butcher site; however, this is debated since only one bone, a rhinoceros mandible, has irrefutable cut marks (Wojtal & Patou-Mathis, 2003). The Skaratki site has the remains of one mammoth, a few flint flakes, and some charcoal, which led the original researchers to suggest it was a mammoth kill site (Wojtal & Patou-Mathis, 2003). However, no cut marks were found on the bones, rendering this interpretation questionable.

Germany

Subsistence and behavioral strategies have been widely investigated in Middle Paleolithic sites throughout Germany, and have provided interesting information concerning Neandertal hunting economies. For example, the northern site of Salzgitter Lebenstedt contained well-preserved lithic and faunal assemblages. Although the majority of the lithic assemblage was comprised of flint Mousterian artifacts, mostly bifacial tools, mammoth bone tools were also found (Gaudzinski, 2000; Gaudzinski & Roebroeks, 2000). Additionally, nearly 3000 faunal remains have been excavated, including the two northernmost-located Neandertal individuals (Gaudzinski, 2000; Gaudzinski & Roebroeks, 2000).

Reindeer dominated the assemblage, with mammoth, horse, bison, and woolly rhinoceros also present (Gaudzinski, 2000; Gaudzinski & Roebroeks, 2000). Not only was reindeer the predominant mammal, but there was also a noticeable difference in their taphonomic history from the other mammals identified (Gaudzinski, 2000; Gaudzinski & Roebroeks, 2000). Namely, the reindeer bone remains were well preserved, and carnivore taphonomic damage, identified through gnaw-marks, was present on less than 2% of the identified elements, and there was evidence of clear hominin modification (Gaudzinski,

2000; Gaudzinski & Roebroeks, 2000). On the other hand, the other mammals in the assemblage demonstrated selective bone preservation and 20% to 70% carnivore damage (Gaudzinski, 2000; Gaudzinski & Roebroeks, 2000).

When the reindeer remains were examined further, 86 individuals were recognized, with the majority represented by adult males taken during autumn (Gaudzinski, 2000; Gaudzinski & Roebroeks, 2000). Human modification was identified by bone fracture patterns as well as cut marks at disarticulation sites, representing marrow procurement and meat processing, respectively (Gaudzinski, 2000; Gaudzinski & Roebroeks, 2000). Interestingly, only adult bones rich in marrow were fractured for marrow procurement, with a selection against adult bones with little marrow and subadult reindeer altogether (Gaudzinski, 2000; Gaudzinski & Roebroeks, 2000). This assemblage suggests intercept hunting of prime-age reindeer by Neandertals, with exploitation of only the highest quality nutritional parts of the animal (Gaudzinski, 2000; Gaudzinski & Roebroeks, 2000).

Parts of the Rhineland, including the Neuwied Basin and Rheinhessen, have also been examined, although bone preservation is limited throughout the area (Conard & Prindiville, 2000). The taphonomic histories at these sites, including layers at Tönchesberg, Metternich, and Rheindahlen, have reduced the amount of bone, leaving only Mousterian lithic artifacts in some cases (Conard & Prindiville, 2000). Moreover, the absence of cut marks on faunal assemblages at nearly all the sites have allowed some to conclude that butchery must have taken place, but depositional processes have obliterated the evidence (Conard & Prindiville, 2000). Regardless, these sites span the entire duration of Neandertal existence, and paleoanthropologists have been able to tease information from the limited data at hand.

The assemblages from the early Middle Paleolithic include layers from Ariendorf, Schweinskopf-Karmelenberg, Wannen, and Tönchesberg, which are all located in the Neuwied Basin (Conard & Prindiville, 2000). At Ariendorf, few lithics were excavated, including cores and unmodified flakes, and, likewise, little faunal remains have been identified (Conard & Prindiville, 2000). Three horses, two woolly rhinoceroses, one mammoth, and two red deer have been found, but cut marks were not identified, and carnivore gnaw marks are prevalent (Conard & Prindiville, 2000).

More information is present at Schweinskopf-Karmelenberg, as nearly the entire lithic assemblage is made from local quartz cobbles (Conard & Prindiville, 2000). Moreover, the fauna are predominantly horse, but woolly rhinoceros, reindeer, and red deer are also present. Adult fauna seemed to be the preferred resource, and little carnivore remains or taphonomic damage is present (Conard & Prindiville, 2000).

Local quartz was also the preferred resource at both Wannen and Tönchesberg, with the majority of the faunal remains again being horse, woolly rhinoceros, and red deer, but reindeer, badger, wolf, and mammoth were also recovered (Conard & Prindiville, 2000). The skeletal element profiles suggest Wannen may have been not only a kill site, but also an area where selective transport occurred from a nearby kill location. Also, although no cut marks are present at Tönchesberg, evidence of fresh bone fragmentation, possibly for marrow extraction, does exist (Conard & Prindiville, 2000).

The late Middle Paleolithic assemblages from the Rhineland include several layers from Wallertheim in Rheinhessen, and Tönchesberg, and Hummerich in the Neuwied Basin. Wallertheim, an open-air site, dates to approximately OIS 5, as suggested by the presence of warm-loving wild cherry, oak, and poplar botanical remains during interstadials and an

absence of botanical remains during stadials (Conard & Prindiville, 2000). The lithic assemblage was dominated by artifacts made of rhyolite (volcanic rock), with a resource cache located approximately 3 kilometers (1.9 miles) from the site (Conard & Prindiville, 2000). The faunal assemblages had fallow deer, horse, and bison, with burned bone, mostly of fallow deer, contained within a hearth area (Conard & Prindiville, 2000). Some evidence of red deer, lion, wild ass, and wolf were also identified within the layers (Conard & Prindiville, 2000).

Evidence for a hearth has also been found at Tönchesberg, with burned fauna and lithics. Locally available quartz was used chiefly at both Tönchesberg and Hummerich, and red deer, horse, and bison dominated the faunal remains at both sites (Conard & Prindiville, 2000). However, rhinoceros, fallow deer, wild ass, lynx, fox, and hyena have been recovered in small amounts at Tönchesberg (Conard & Prindiville, 2000).

Overall, the sites from the Rhineland of Germany are affected differentially by taphonomic processes, making interpretations difficult in some areas; however, some inferences can be made. For example, while bison, horses, and deer were consistently taken throughout time, rhinoceros was predominantly found in the earlier assemblages, and mammoth was exclusively so (Conard & Prindiville, 2000). Another inference is differences in animal transport strategies between the sites, with reference to elevation. The higher-elevation sites had skeletal element profiles indicating that mammals were killed off-site, and their limbs transported back, while those in lower areas suggested the animals were killed at the site (Conard & Prindiville, 2000). Lastly, seasonality can be inferred from faunal tooth cementum, and these data indicated different occupations at different times of the year (Conard & Prindiville, 2000).

Southern German cave sites, specifically those in the Lone Valley, have also been examined, including Haldensteinhöhle, Bockstein, Bocksteinhöhle, Bocksteintörle, Bocksteinschmiede, Hohlenstein-Bärenhöhle, Hohlenstein-Stadel, and Vogelherd (Krönneck et al., 2004). Collective charcoal and botanical remains from these sites suggested an oscillating climate between warm-loving oak, hornbeam, maple trees, and colder, steppe environments (Krönneck et al., 2004).

The faunal assemblages differed between sites, with as few as 200 to as many as 2,000 remains; however, some commonalities still exist (Krönneck et al., 2004). Specifically, cave bear was found at all sites, but only predominated at Hohlenstein-Stadel. Large herbivores such as woolly mammoth and rhinoceros were present, as well as horse, red and giant deer, reindeer, bison, ibex, and wild boar, and carnivores such as cave hyena, red and arctic fox, wolf, lion, and wolverine (Krönneck et al., 2004).

More specifically, the larger assemblages at Bockstine, Vogelherd, and Hohlenstein-Stadel, were dominated by horse, but reindeer, woolly rhinoceros, and cave hyena followed as the next common species, respectively (Krönneck et al., 2004). These assemblages also suggested a competition between carnivores and Neandertals for both the sites themselves as well as the nearby prey animals, making interpretations as to who contributed to the faunal assemblages uncertain (Krönneck et al., 2004). However, the predominance of horse remains, especially at Bockstein, suggest Neandertals preferred this resource, and practiced intercept hunting to procure it (Krönneck et al., 2004).

Lastly, southwestern German cave sites in the Ach Valley have been investigated for differences between Middle and Upper Paleolithic strategies (Münzel & Conard, 2004). The

Ach Valley sites include Geißenklösterle, Sirgenstein, Große Grotte, and Kogelstein, and range in chronology from approximately 45,000 BP to 13,000 BP (Münzel & Conard, 2004).

Geißenklösterle spanned this entire temporal range, with carved ivory and bone implements found in the Aurignacian layers, and low densities of artifacts in earlier, Middle Paleolithic deposits due to poor preservation (Münzel & Conard, 2004). The faunal assemblages change from the Middle to Upper Paleolithic, with cave bear overwhelmingly dominating the Middle Paleolithic assemblage, and bison, red/arctic fox, mammoth, horse, reindeer, and ibex also included (Münzel & Conard, 2004). The Upper Paleolithic assemblage also frequently had mammoth, reindeer, and horse, but the percentage of cave bear, along with other medium-to-large carnivores decreased (Münzel & Conard, 2004). Moreover, although Neandertal modification was present in the form of burned bone and cut and impact marks, there was an abundance of human modification evidence in the Upper Paleolithic layers, mostly in the form of carved ivory objects or bone implements (Münzel & Conard, 2004).

Sirgenstein cave has yielded Middle Paleolithic layers, and the faunal assemblage has been described as consisting of 90% cave bear, although many of the specimens are missing (Münzel & Conard, 2004). Horse, reindeer, giant deer, and mammoth were also represented in these layers, with impact fractures and cut marks found on several of the remains, and several hearths found (Münzel & Conard, 2004). Seasonality, based on juvenile horse remains, suggests a winter occupation (Münzel & Conard, 2004).

Große Grotte and Kogelstein also contained Middle Paleolithic layers, but were dominated by cave bear and hyena remains, respectively. Ibex and reindeer were also present at Große Grotte, but 30% of the remains have carnivore gnaw marks (Münzel &

Conard, 2004). Although this is suggestive of a cave bear den, there are some indications of Neandertal activity, such as the presence of burned bone, worked antler point, and mammoth-rib tool (Münzel & Conard, 2004). Kogelstein had a lower incidence of bear, but hyena and fox were present, along with horse and deer (Münzel & Conard, 2004). Neandertal activity is also proposed given cut and impact marks on several bones (Münzel & Conard, 2004).

Overall, the Ach Valley sites are dominated by carnivores, especially cave bear, but human activity is also found. Differences between Middle and Upper Paleolithic hominins, as evidenced by assemblages at Geißenklösterle, are predicted to be due to variance in tool production (Münzel & Conard, 2004). For example, fewer mammoth remains were found in the Middle Paleolithic layers than in later ones because they were not used for bone points or ivory implements (Münzel & Conard, 2004). Moreover, butchering practices were most likely different between these two hominins, as bone and ivory taken for tool production requires more cutting and cleaning, resulting in increased cut marks and striations on these bones (Münzel & Conard, 2004). The absence of cut marks on Neandertal-taken fauna may be due to this phenomenon.

Italy and France

Italy has cave, rock shelter, and open-air Neandertal sites that range from approximately 160,000 to 30,000 BP. While these sites are found in both coastal and interior areas within a range of elevations, caves and rock shelters are better preserved as they are not as affected by depositional processes as the open-air sites (Fiore et al., 2004). Consequently, the majority of assemblages are found in caves and rock shelters.

Northeastern Italian cave and rock shelter sites are mostly found in the piedmont slopes of the Italian Alps, and include Ripara Tagliente, Riparo Mezzena, Grotta Maggiore di

S. Bernardino, and Grotta di Fumane (Fiore et al., 2004). These sites are characterized by Levallois Mousterian tool industries, and thick stratigraphic layers support the occupation of these sites over a long period of time (Fiore et al., 2004).

Ripara Tagliente dates to OIS 3, and the oscillating climate conditions can be inferred from the mammal and micromammal frequencies. First, the medium-to-large mammal assemblage consists of red and roe deer, with some elk and marmot (groundhog) remains also present (Fiore et al., 2004). Modification to these bones are abundant, providing evidence that Neandertals were at least partially responsible for the accumulation of the assemblage (Fiore et al., 2004). The micromammal remains have been more completely examined, and provide evidence for fluctuations in the area between forest and woodland areas to dry, steppe environments, back to more humid open or woody grassland (Fiore et al., 2004).

The Ripara Mezzena rock shelter is located near Verona, and the fauna represented include marmot, red, roe, and giant deer, wild boar, and carnivores such as bear, hyena, wild cat, fox, and wolf (Fiore et al., 2004). The micromammal remains are mostly those associated with forest environments, but some steppe rodents are also present (Fiore et al., 2004).

Grotta Maggiore di S. Bernardino and Grotta di Fumane have been more extensively studied. Grotta Maggiore di S. Bernardino contains both Middle and early Upper Pleistocene horizons, both with Mousterian lithics (Fiore et al., 2004). Although more than 14,000 faunal specimens have been recovered, only 10% could be identified to the genus or species level due to the extensive fragmentation of the bones (Fiore et al., 2004). However, the identified faunal remains are dominated by ungulates, including red and roe deer, chamois

(goat-antelope), ibex, elk, and giant deer, but carnivores such as cave bear, fox, wolf, lynx, and leopard are also represented (Fiore et al., 2004). Smaller mammals such as hare, beaver, wild boar, marmot, as well as birds, are also present (Fiore et al., 2004).

It is clear from both the cave bear remains and the carnivore gnaw marks on the other faunal remains that the cave site oscillated between a bear den and Neandertal shelter (Fiore et al., 2004). Additionally, the cut marks on the ungulate remains suggested Neandertals used these resources for food; this is supported by the mortality profiles that indicated these mammals were young adult and adult individuals (Fiore et al., 2004). Moreover, cut marks found on beaver remains indicated the fur was used for pelts (Fiore et al., 2004).

Grotta di Fumane has Upper Pleistocene deposits, with Mousterian tools dating from 80,000 to 38,000 BP (Fiore et al., 2004). Approximately 160,000 faunal specimens have been excavated, but only 4.5% of the assemblage have been identified to the genus or species level (Fiore et al., 2004). Additionally, cut marks and burned bone, as well as carnivore gnaw marks are present, suggesting a combination of hominin and carnivore accumulation (Fiore et al., 2004). The ungulates included red and roe deer and ibex, with chamois, giant deer, and bison also represented, and, again, young adult and adult individuals make up the majority of the assemblage (Fiore et al., 2004). The carnivore remains included cave and brown bear, red fox, hyena, and wolf (Fiore et al., 2004). Although 35 different species of birds were identified, it is unclear whether their presence is due to hominin, carnivore, or birds of prey activity; however, one golden eagle phalanx[11] had stone tool cut marks, which has been tentatively interpreted as evidence for using the talon as an ornament (Fiore et al., 2004).

[11] Similar striations have also been found on a golden eagle phalanx from Pech de l'Aze in France (Fiore et al., 2004).

The northeastern Italian cave and rock shelter sites can provide evidence for Neandertal subsistence strategies, especially as they coincide with changing climate conditions. For example, the micromammal remains at several sites demonstrate a shift between mainly woodland with temperate climates and colder, drier, steppe environments (Fiore et al., 2004). This can be buttressed by the change in ungulate frequencies, such as the transition between red and roe deer, which indicate temperate woodlands, and ibex and chamois, which suggest cold and dry steppe or grassland (Fiore et al., 2004). Neandertals preferred to exploit young adult and adult individuals, suggesting intercept hunting of animal resources, as well as the taking of smaller mammals, such as beaver and hare, for pelts (Fiore et al., 2004).

West-central coastal sites on the Tyrrhenian Sea, south of Rome, consist of both open-air and shallow cave sites. Although the open-air localities have been subjected to heavy erosion and show few artifacts, cave sites often have thick occupational layers, suggesting repeated occupancy (Stiner, 1994). Two nearby promontories contained collections of shallow cave sites, including the more northern Monte Circeo sites of Grotta Breuil and Grotta Guattari, and those near Gaeta, including Grotta di Sant'Agostino and Grotta dei Moscerini (Stiner, 1994). The landscape allowed for a mild climate and rich ecological diversity, and the combination of these two factors has often been cited as the reason why Neandertals continuously returned to these locations.

The lithic assemblages in this area are Mousterian, but represent a smaller size tool tradition than those seen in other areas (Stiner, 1994). The size of these tools, which measure a maximum of three centimeters in any dimension, are generally believed to be a consequence of the locally available, tiny flint cobbles and lack of other raw materials in the

area (Stiner, 1994). Indeed, the paucity of raw material led to interesting ingenuities, such as the utilization of marine clam shells as simple scrapers (Stiner, 1994).

Grotta Breuil had an abundance of ungulates, with minimal evidence for carnivore remains (Stiner, 1994). Red deer and ibex comprised the majority of the assemblage, with roe deer, fallow deer, aurochs, and horse also present, along with low quantities of wild ass, chamois, elephant, and rhinoceros (Stiner, 1994). Carnivore remains consisted mostly of wolf, but brown bear, wild cat, red fox, and spotted hyena were also present (Stiner, 1994).

Grotta Guattari, famous for its indications of Neandertal ritual and possible cannibalism, demonstrated red deer as the predominant species, with aurochs and fallow deer following in second and third, respectively (Stiner, 1994). Horse and roe deer were also somewhat common, with roe deer, wild boar, rhinoceros, and elephant appearing in lower incidences (Stiner, 1994). Carnivores, common in the earlier layers of the site, consisted primarily of spotted hyena, and cave bear, with leopard and wolf also appearing (Stiner, 1994).

Grotta di Sant'Agostino also preserved large numbers of red deer, followed by nearly equal frequencies of fallow and roe deer (Stiner, 1994). Ibex and wild boar were also somewhat frequent, along with aurochs, and horse and rhinoceros had low representation (Stiner, 1994). The majority of the carnivore remains consisted of red fox, but wild cat, wolf, brown bear were also present, with low frequencies of weasel, badger, and leopard (Stiner, 1994).

Grotta dei Moscerini faunal assemblages were dominated by ungulates, with red deer most common, followed by roe deer, and horse, rhinoceros, hippopotamus, fallow deer, ibex, wild boar, and aurochs appearing at lower frequencies (Stiner, 1994). Few carnivores were

present except in one layer where they dominate the assemblage (M5), with brown bear and spotted hyena contributing the most, and fox and wild cat also present (Stiner, 1994).

The cave sites from west-central coastal Italy showed a diversity in landscapes reflected by the range of available fauna from which Neandertals had to choose. While these sites were undoubtedly affected by changing climate conditions through time, the consistent nature of animal species present throughout the occupational horizons attest to the minimal affect these changes had on the vegetation and fauna (Stiner, 1994). Although a variety of mammals made up the faunal assemblages, these four sites demonstrated a consistent preference towards red deer. While carnivores may be partially responsible for the accumulation of these ungulates to the sites, the lithic tool assemblages associated with these remains, along with burned bone and other evidence of human modification suggested Neandertals preferred these mammals as sources of food (Stiner, 1994).

Middle Paleolithic sites from the Mediterranean coast, such as Arma delle Manie, Caverna delle Fate, Santa Lucia Superiore, San Francesco, and Madonna dell'Arma of northwestern Italy and Grotte du Prince and Grotte du Lazaret of southeastern France, have been examined for patterns of faunal exploitation as well (Valensi & Psathi, 2004). These sites, which date from OIS 6 to OIS 3, have faunal assemblages that reflect a range of habitats, from grassland to forests; however, the variety of represented fauna also suggested a continuity of resources, so much so that climate variability, although undoubtedly present, was not dramatic enough to remove most species from the environment (Boyle, 2000; Valensi & Psathi, 2004). This suggested that these coastal offered refuge for warm-loving vegetation and fauna, even during cold intervals.

Red deer dominate the assemblages of five of these sites, with Caverna delle Fate having more roe deer and Santa Lucia Superiore having more mountainous taxa, such as ibex and chamois, due to its elevation (Boyle, 2000; Valensi, 2000; Valensi & Psathi, 2004). Carnivores, such as cave bear, are also present, and there are several examples of stone tool cut marks on their bones at Caverna delle Fate, Madonna dell'Arma, and Arma delle Manie (Valensi & Psathi, 2004). It is suggested that these cut marks either indicated hunting of the cave bear, or opportunistic acquisition of fur and/or meat resources (Valensi & Psathi, 2004). Moreover, mortality profiles at the majority of the sites indicated prime-aged adult ungulates were preferentially taken, although the reason for this preference could be interpreted as intercept hunting or merely a sheer abundance of such animals (Boyle, 2000; Valensi, 2000; Valensi & Psathi, 2004).

Middle Paleolithic sites further west along the French Mediterranean coast, including those dated to more temperate OIS periods (Grotte du Lazaret, Grotte des Cèdres, Adaouste, and Les Canalettes) and those in colder OIS times (Hortus, Salpêtre de Pompignan, Mauran, and Tournal) have been examined under both a paleoenvironmental and paleoeconomic lens (Boyle, 2000).

These sites suggested variation in environmental conditions, with faunal assemblages spanning a range of locally available resources (Boyle, 2000). Those sites located within more open, colder montane or cliff-face areas, especially Hortus and Salpêtre de Pompignan, had higher proportions of ibex, which is well-adapted to this type of geography (Boyle, 2000). However, woodland-adapted ungulates, such as red and roe deer, reindeer, aurochs, horse, and wild ass were also represented, along with wolf, fox, lynx, cave bear, and leopard (Boyle, 2000). Those sites suggested to be more forested environments, such as Grotte du

Lazaret, had mostly red deer, but more montane species, such as ibex and chamois, were also present (Boyle, 2000). Identifiable cut marks, percussion blows, and other forms of human modification were present at all sites, suggesting Neandertals practiced a variable exploitation strategy within a diverse ecozone, not unlike the circulating mobility strategy proposed for AMH by Lieberman and Shea (Lieberman & Shea, 1994; Boyle, 2000).

Although dietary and behavioral strategies are suggested indirectly by lithic and faunal assemblage types, some researchers have developed functional analyses in order to directly gauge for and on what these tools were used. Indeed, several studies of southern French Mousterian tools have undergone microwear analyses in order to better understand and interpret what materials were being manipulated with these lithics (Anderson-Gerfaud, 1990; Hardy, 2004).

Tool microwear analyses are different from dental microwear in the range of magnifications used to discern larger features, such as chipping and rounding, from smaller characteristics, such as material and animal residues (Anderson-Gerfaud, 1990; Hardy, 2004). Moreover, experimental tool production and use has offered comparative baselines series for the fossil lithic assemblages, making inferences about hominin tool use more concrete (Anderson-Gerfaud, 1990).

Using lithic assemblages from several southwestern French sites, including Corbiac, Pech de l'Aze, and Combe Grenal, it was determined that none preserved evidence of projectile use and few demonstrated butchery, providing support for limited Neandertal hunting capabilities (Anderson-Gerfaud, 1990). However, several different types of tools, including all of the denticulates, suggested woodworking, which could garner support for spear production (Anderson-Gerfaud, 1990). That is, hunting may have been carried out, but

with organic materials that did not preserve; in fact, evidence for wooden spear use has been documented at several sites, including Clacton-on-Sea, Lehringen, and Schöningen (Conard & Prindivelle, 2000).

Hide preparation was also examined, and nearly 10% of the retouched tools displayed evidence for it (Anderson-Gerfaud, 1990). Although all the tool types were different, they basically conformed to convex-edged side- or endscrapers (Anderson-Gerfaud, 1990). Alaskan Eskimo and Canadian and Greenland Inuit populations, specifically females, have also been documented using stone tools to prepare hides, and use their anterior dentition as a third hand while completing these tasks (Griffen, 1930; Anderson-Gerfaud, 1990; Foote, 1992).

Evidence for plant resource use is difficult to discern in the fossil record, however, a few tools were shown to reflect cutting or scraping of soft plant material (Anderson-Gerfaud, 1990). One convex scraper from Combe Grenal preserved not only indications of hafting, but also a phytolith on the working side (Anderson-Gerfaud, 1990). This phytolith was identified as either a grass or sedge, and provides a direct signal of seed collection, or use of these resources for basketry or fuel (Anderson-Gerfaud, 1990).

Microwear tool analyses have also been completed at the Mousterian Neandertal site of La Quina, with faunal assemblages also taken into consideration (Hardy, 2004). La Quina, located in interior southwestern France, yielded an extensive collection of lithic, faunal, and hominin assemblages, and dates to approximately OIS 4-3 (Hardy, 2004). The faunal remains consisted of horse, bison, and reindeer, suggesting consistently cold, open steppe environmental conditions; this was buttressed by low levels of arboreal pollen (Hardy, 2004).

Of the 300 lithics examined, 148 of them possessed use-wear and/or residues, with use-wear most commonly identified as polishes relating to contact with wood, bone, antler, or grass, while 12 others displayed polishes indicative of hide or herbaceous plants (Hardy, 2004). The differences in polishes were inferred from several experimental baseline series. Additionally, several different categories of plant residues were discovered, including plant tissues, pollen, raphides, and wood fiber (Hardy, 2004). Animal residues were less common, but included blood, hair, bone, antler, and feathers; in fact, in some cases, both plant and animal residues were found on the same tool (Hardy, 2004).

Neandertal behavior at La Quina can be better interpreted with the microwear analyses of these tools. First, these hominins were exploiting a range of available resources, including plants, animals, and birds (Hardy, 2004). Second, the presence of both plant and animal residues on the same tool indicated an industry that was multi-functional, refuting ideas of one-to-one associations between tool form and function (Hardy, 2004). Third, the bone and antler residues suggest the Neandertals at La Quina were either using these resources as retouchers or hammers in stone tool production, or using the stone tools to modify these resources (Hardy, 2004). Finally, DNA amplification on blood residues has pinpointed the source to be pig or boar, supporting the notion, along with the hair and feather residues, of capable Neandertal hunting behavior (Hardy, 2004).

Iberia and Gibraltar

Several sites in and around the Iberian Peninsula have provided interesting data about Neandertal behavior. For example, integrative analyses of Abric Romaní, a rock shelter in northeastern Spain, have been able to describe Neandertal behavior in a comprehensive manner (Vaquero et al. 2001). The 27 occupational horizons at this site all date to the

Middle Paleolithic except for the uppermost layer, which dates to the early Upper Paleolithic (Vaquero et al. 2001).

These layers, which date to the very end of OIS 5 through 3, were dominated by flint flakes and their fragments, but quartz and limestone were also common, especially in the earlier layers (Vaquero et al. 2001). Quartzite, sandstone, and porphyry materials were found in fewer quantities (Vaquero et al. 2001). Interestingly, these raw materials were all found locally, with the flint resource located the furthest from the site, at a distance of five kilometers (3.1 miles) away (Vaquero et al. 2001).

Use-wear analyses of the retouched tools, which mostly consisted of denticulates, but also sidescrapers, endscrapers, etc., coincided with those of Hardy (2004). Specifically, the form did not dictate the function, and denticulates were used for both woodworking and animal processing (Vaquero et al. 2001). Moreover, these Neandertals showed heavy tool use, with 87% of tools from one occupational layer alone demonstrating use-wear (Vaquero et al. 2001).

The faunal assemblage was dominated by horse and red deer in every level, although aurochs and rhinoceros were present in some layers (Vaquero et al. 2001). This suggested the area consisted of plains and more open woodland environments. Cut and percussion marks were common, with the cut marks suggestive of herbivore processing, with defleshing and scraping features found on bones of all sizes (Vaquero et al. 2001). Evidence for percussion was found not only with a lack of epiphyses present, but also the longitudinal fracturing of diaphyses of all sizes (Vaquero et al. 2001). Although the number varied by occupational layer, there was also indications of human modification through burned bone (Vaquero et al. 2001). Lastly, Neandertals were suggested to be the primary agent for faunal

accumulation, as carnivore gnaw marks were only found on 5% of the bones (Vaquero et al. 2001).

More and more research is being devoted to the use of plant resources in hominin daily lives. Indeed, Abric Romaní is a rich source for charcoal and wood remains, providing important and rarely found archaeobotanical data. Charcoal from the earlier layers demonstrated that pine was the sole resource used, and it continued to be the most common resource in later levels (Vaquero et al. 2001). In addition, charred pine and juniper wooden artifacts, interpreted as possible domestic implements, and casts of wood, probably related to firewood and woodworking, have also been recovered (Vaquero et al. 2001). The nearly complete use of pine materials was most likely due to seasonal occupation, and reflected the most commonly found local resource (Vaquero et al. 2001).

Iberia is also recognized as having late Neandertal sites, including Zafarraya in Spain, Devil's Tower in Gibraltar, and Gruta da Figueira Brava in Portugal (Antunes et al., 2000). This last site, dated to approximately 30,000 years BP, has been the subject of several papers and lines of research because it demonstrates differences in Neandertal behavior from those previously discussed. Namely, there is evidence for marine resource exploitation (Antunes, 2000a; Antunes et al., 2000).

The Mousterian lithic assemblage at Gruta da Figueira Brava consisted of over 4,000 artifacts, and the raw materials consisted of locally and regionally available quartz, flint, jasperoid, and limestone (Raposo & Cardoso, 2000). Flakes and cores were present, as well as retouched tools such as several types of scrapers, burins, backed knives, notches, denticulates, retouched flakes, and choppers (Raposo & Cardoso, 2000). Tools have also been recovered that are typically found in Upper Paleolithic contexts, including those made

from bone, antler, and teeth (Antunes, 2000b). These tools were produced from a variety of mammals, including red deer, horse, goat, auroch, hyena, and rabbit (Antunes, 2000b).

The fauna mirrored the unique tool assemblage, with medium-to-large mammals such as red deer, Spanish ibex, auroch, horse, rhinoceros, and woolly mammoth represented; however, the red deer and Spanish ibex made up the majority of the collection (Antunes, 2000c). Interestingly, remains from one ringed seal and six common dolphins were also recovered, providing evidence for sea mammal exploitation (Antunes, 2000c). Use of sea resources were also supported by recovery of snails, mussels, clams, crabs, and sea urchins (Antunes, 2000c).

Sites on Gibraltar also support the exploitation of marine resources by Neandertals, and for a longer period of time than at Gruta da Figueira Brava (Stringer et al., 2008). Vanguard and Gorham's Caves, located on the eastern side of the island, date to OIS 5-3 and both show evidence for a wide range of terrestrial, marine, and avian resource exploitation (Stringer et al., 2008).

Vanguard Cave layers contained Mousterian stone tools and debitage mixed with mussel shells and hearths (Stringer et al., 2008). Commonly recovered terrestrial fauna, such as red deer, ibex, bear, and wild boar were present, but seals, dolphins, mollusks, birds, tortoise, and fish were also found (Stringer et al., 2008). Defleshing cut marks identified on the seal remains provided additional support for use of these resources by Neandertals (Stringer et al., 2008). Cut marks and percussion blows were also found on the terrestrial mammal remains, and less than 3% were affected by carnivore gnaw marks (Stringer et al., 2008).

Gorham's Cave demonstrated similar patterns as those found at Vanguard Cave. Namely, Mousterian lithic tools and debitage were found in conjunction with red deer, ibex, horse, seals, fish, and birds (Stringer et al., 2008). Moreover, cut marks and percussion blows, indicative of butchering, filleting, and marrow extraction have been identified, and carnivore damage is negligible (Stringer et al., 2008).

Summary

Overall, Neandertal subsistence and behavioral strategies varied according to time, space, environmental conditions, available ecological zones, locally available lithic raw materials, and faunal accessibility. Admittedly, accounting for and addressing the role each variable plays at any given site is a daunting task for any paleoanthropologist. However, the identification and recognition of these different variables speaks to the ability of Neandertals to successfully live and subsist under the umbrella of changing conditions.

The review of lithic and faunal assemblages spanning the time and space of Neandertal existence has generated some common threads. First, Mousterian tools seem to be strongly associated with Neandertals. Although differences in this lithic industry is beyond the scope of this review, the Mousterian tool tradition is basically comprised of various scraper types, notches, backed knives, and denticulates, with microwear evidence of these retouched tools suggesting woodworking and butchery. Moreover, Neandertals most often utilized local raw materials for production of their tools, and non-local materials are rare.

Neandertal faunal preferences, although biased by intermittent carnivore activity at most sites, seemed to be focused on medium-to-large sized terrestrial mammals. Red deer was by far the most commonly taken species, but wild goat, ibex, aurochs, bison, rhinoceros,

woolly mammoth, red deer, and giant deer were commonly found as well. Many faunal assemblages can suggest environmental conditions, and, when used in conjunction with more reliable forms of paleoclimate reconstruction, can help discern seasonality in Neandertal occupation. Later Neandertal sites found in the Iberian Peninsula area demonstrated Neandertal adaptability with an expanded range of exploited fauna, including fish, shellfish, birds, and sea mammals, along with commonly found terrestrial mammals as well.

The debate surrounding Neandertal hunting or scavenging can be confusing, especially when evidence could be interpreted in more than one way. For example, several studies have focused on the abundance of red deer at the particular site being described. The most proposed explanation for this preference is intercept hunting of prime-aged adults, suggesting Neandertals would not commonly participate in encounter hunting, and would, consequently, spend more time and energy focused on one type of animal (Steele, 2004). However, couldn't the abundance of red deer simply signal an abundance of this resource? Also, what about post-depositional processes, which may favor the preservation of prime-aged adults over those of juveniles?

Regardless, the majority of lithic and faunal assemblage studies strongly support Neandertals as capable hunters. Does this mean they never scavenged? Absolutely not. It only means they were cognitively and behaviorally complex enough to have produced effective hunting and butchery tools, as well as produce fire and accumulate a wide range of fauna in their shelters. There is even evidence for the use of plant materials in spear production, domestic implements, bedding, and fuel. The continuation of innovative research in animal and plant resource exploitation by Neandertals will no doubt uncover additional evidence of their dietary and behavioral breadth.

Direct evidence

Lithic and faunal assemblages are the conventional forms of dietary and behavioral reconstruction, and can provide important clues to the strategies of Neandertals and anatomically modern humans; however, there are concerns surrounding these indirect forms of reconstruction. First, the majority of lithic assemblages are found at cave sites, where they can undergo geological processes, such as cryoturbation and bioturbation, over time. These processes can alter the stratigraphic sequences, making inferences about behavior, preference, or change through time difficult at best (Lee-Thorp & Sponheimer, 2006). Second, faunal assemblages and the mode of their accumulation has been questioned. While both the accumulation and taphonomic damage of opportunistic carnivores has been accounted for in more recent research, some still question the role hominins played in faunal procurement (Lee-Thorp & Sponheimer, 2006). Lastly, these lines of evidence focus predominantly on meat resources, even though plants usually made up the majority of hominin diets (Lee-Thorp & Sponheimer, 2006). As a result of these challenges, several lines of direct dietary and behavioral evidence has been developed. Neandertals and anatomically modern humans have been studied using two methods: stable isotope and dental microwear analyses.

Direct evidence: stable isotope analyses

Stable isotope analysis is one method in a suite of techniques known as chemical dietary indicators, and is the most often used method in Neandertal and anatomically modern human dietary analyses. The underlying premise is that dietary elements, specifically carbon and nitrogen, are incorporated into the production of bone collagen and apatite, and can

indicate diet and environment (Bocherens, 1997; Lee-Thorp & Sponheimer, 2006). Bone collagen undergoes a turnover rate, and indicates diet over several years, while dental apatite only indicates diet during crown development (Bocherens, 1997).

As indicated by the name, stable isotope analyses only examine the stable, as opposed to the radioactive, isotopes of carbon and nitrogen. Specifically, the *ratio* of heavier to lighter stable isotopes are analyzed, with the heavy isotopes being ^{13}C and ^{15}N, and the light isotopes being ^{12}C and ^{14}N (Bocherens, 1997). Thus, the stable isotope ratios are $^{13}C/^{12}C$ and $^{15}N/^{14}N$. Once these ratios are determined for any given sample, they are compared with an international standard and the stable isotope abundance, denoted as delta or δ, is calculated using the equation:

$$\delta^{E}X = (R_{sample} / R_{standard} - 1) \text{ X } 1000 \text{ (‰)}$$

where X is C or N, E is 13 or 15, and R is the ratio of heavier-to-lighter isotopes (Bocherens, 1997; Lee-Thorpe & Sponheimer, 2006). Since the difference in ratios between the sample and standard is so small, they are expressed as parts per thousand, denoted as ‰. For example, to determine the amount of ^{13}C and ^{15}N in a sample, the equations would be:

$$\delta^{13}C = \{(^{13}C/^{12}C_{\text{ sample}}) / (^{13}C/^{12}C_{\text{ standard}}) - 1\} \text{ X } 1000 \text{ (‰) and}$$

$$\delta^{15}N = \{(^{15}N/^{14}N_{\text{ sample}}) / (^{15}N/^{14}N_{\text{ standard}}) - 1\} \text{ X } 1000 \text{ (‰), respectively.}$$

Since bone collagen and apatite have less ^{13}C than ^{12}C, these values are negative, but bone collagen and apatite favor ^{15}N over ^{14}N, providing positive values (Bocherens, 1997).

The next aspect to stable isotope analyses is how $\delta^{13}C$ and $\delta^{15}N$ values found in bone collagen relate to diet. The $\delta^{13}C$ values found in animal tissue are slightly higher than those of the food it eats (Bocherens, 1997; Dorozynski & Anderson, 1991). For example, there is a steady increase in $\delta^{13}C$ values from plants to herbivores to carnivores, with different base

levels depending on geographic location (Richards & Trinkaus, 2009). Interestingly, plant $\delta^{13}C$ values demonstrate a bimodal distribution, which relates to two different photosynthetic pathways.

A terrestrial plant converts carbon dioxide into sugar during photosynthesis, and while this process discriminates against ^{13}C found in CO_2, it does so differently depending on the pathway the plant uses. The C_3 pathway is used by trees, plants, shrubs, and herbs that grow in temperate, cold, and shade-heavy environments and show $\delta^{13}C$ values that average -27.1 ± 2.0 ‰ (Bocherens, 1997; Lee-Thorpe & Sponheimer, 2006). On the other hand, the C_4 pathway is utilized by herbaceous plants and tropical grasses in hot and dry environments, and their $\delta^{13}C$ values are much higher, averaging -13.1 ± 1.2 ‰ (Bocherens, 1997; Lee-Thorpe & Sponheimer, 2006). As a result of these contrasting $\delta^{13}C$ values, the type of plant favored by an herbivore or the type of herbivore prey favored by a carnivore can be examined through the analysis of the $\delta^{13}C$ values recorded in their bone collagen.

There is a third type of photosynthetic pathway used by desert succulents, known as CAM (Crassulacean Acid Metabolism) (Bocherens, 1997). These plants alternate their use of C_3 and C_4 pathways, and consequently, their $\delta^{13}C$ values vary considerably depending on environmental conditions (Bocherens, 1997; Lee-Thorpe & Sponheimer, 2006). Since hominin use of these plants is thought to be minimal, CAM plants are not generally considered in analyses (Lee-Thorpe & Sponheimer, 2006).

Studies of $\delta^{13}C$ values have been minimally useful in Neandertal and anatomically modern human bone collagen research because all native European plants use the C_3 pathway (Lee-Thorpe & Sponheimer, 2006). However, $\delta^{15}N$ values have been exceptionally telling of these hominins' dietary preference.

Nitrogen isotopes enter the food web through soil, and plants absorb the element to make amino acids for the production of proteins. The amount of nitrogen found in the plant is considerably greater than that in the soil. Likewise, the amount of nitrogen found in the herbivore that eats the plant is also greatly increased. This enrichment in $\delta^{15}N$ continues up the trophic web levels, and provides a means of understanding the position an animal maintains in the food web (Bocherens, 1997; Dorozynski & Anderson, 1991; Lee-Thorpe & Sponheimer, 2006).

Terrestrial herbivores demonstrate $\delta^{15}N$ values between 2 to 7 ‰, terrestrial carnivores range from 7 to 12 ‰, and marine mammals are approximately 12 to 20 ‰ (Bocherens, 1997). The higher $\delta^{15}N$ levels in marine mammals are due to a longer food chain found in aquatic environments, as well as a higher retention of ^{15}N in these organisms (Bocherens et al., 1991). It is also interesting to note that nursing mammals are raised a trophic web level, and will have correspondingly raised $\delta^{15}N$ values for up to two years after weaning (Bocherens et al. 1991; Fizet et al., 1995; Bocherens et al., 2001, 2005).

A challenge to $\delta^{15}N$ analyses is that, like carbon, nitrogen levels are geographically heterogeneous, so local, comparative material that ranges across trophic web levels are imperative for proper interpretation of the sample at hand (Bocherens, 1997; Lee-Thorpe & Sponheimer, 2006; Richards & Trinkaus, 2009). Moreover, because nitrogen is a main component in amino acid and protein production, it is favored in bone collagen, allowing for bias in animal over plant-based foods (Bocherens et al., 2005; Lee-Thorpe & Sponheimer, 2006). However, bone collagen can survive for up to 200,000 years, and several studies have demonstrated that quality results can be obtained, providing direct evidence for hominin diets (Lee-Thorpe & Sponheimer, 2006).

The first Neandertal bone collagen study was completed in 1991, and included both faunal and Neandertal remains from Marillac (Les Pradelles) in France (Bocherens et al. 1991). Eleven out of twelve stratigraphic layers at Marillac included Mousterian lithics, and reindeer, auroch, horse, marmot, fox, hyena, and wolf were identified at the site, which dates to approximately 40,000-45,000 BP (Bocherens et al., 1991; Fizet et al., 1995). The $\delta^{13}C$ values for all the mammals listed above, including the Neandertal, range from -21.8 to -18.5 ‰, with the carnivores showing a slightly higher average value than that of the herbivores (Bocherens et al., 1991).

The $\delta^{15}N$ values vary considerably between the herbivores and carnivores, with averages of 4.5 ± 1.7 ‰ and 9.5 ± 0.9 ‰, respectively (Bocherens et al., 1991). The Neandertal $\delta^{15}N$ value was 9.3 ‰, indicating carnivory (Bocherens et al., 1991). A follow-up study of Marillac confirmed these results, and suggested the two Neandertals examined in that study were less specific in their prey selection than the wolf, whose $\delta^{15}N$ values indicated a preference toward reindeer (Fizet et al., 1995). This might provide evidence for encounter over intercept hunting of Neandertals, at least those at Marillac.

Isotopic analyses of Belgian Neandertal remains have also been completed. Bocherens et al. (1999) completed carbon and nitrogen analyses on the Neandertal remains from layer 4 at Scladina, which dates to approximately OIS 5e[12]. In addition to the Neandertal specimen, bone collagen was analyzed from horse, fallow deer, bear, fox, cave lion, hyena, and wolf (Bocherens et al., 1999). The $\delta^{13}C$ values for all species ranged from -25.1 to -18.6 ‰, with the carnivores showing a higher average value than that of the herbivores, a similar situation to what was found at Marillac (Bocherens et al., 1999). The

[12] Although some contend, based on pollen sequences, that this individual dates to approximately 80,000 years BP (Bocherens et al., 1999).

Neandertal value was -19.9 ‰ , which was intermediate between the carnivore (cave lion, cave hyena, and wolf) and fox samples (Bocherens et al., 1999).

The $\delta^{15}N$ values for all species varied from 3.0 to 10.9 ‰, with carnivores having the highest average value, followed in decreasing values by herbivores, foxes, and cave bear (Bocherens et al., 1999). The low values for foxes and cave bear suggest that these mammals relied on more plant-based diets during the warm interglacial period; however, the high $\delta^{15}N$ values found for the Neandertal specimen clearly demonstrates carnivory (Bocherens et al., 1999). The similar $\delta^{13}C$ and $\delta^{15}N$ values for the Marillac and Scladina Neandertals were surprising considering the contrasting paleoclimate reconstructions for each site, and the similar signatures was interpreting as indicating a similar reliance on open-environment herbivores (Bocherens et al., 1999).

Stable isotope analyses of Neandertals from other Belgian sites, including another specimen from Scladina, one from Spy, and a five-to-six-year-old child from Engis, were examined (Bocherens et al., 2001). The $\delta^{13}C$ values for all three specimens were similar to the fauna at Scladina Cave, and ranged from -21.2 to -19.6 ‰ (Bocherens et al., 2001). The $\delta^{15}N$ values were all high, varying from 11.0-12.6 ‰; however, the Engis child exhibited the highest value of 12.6 ‰, which is most likely due to the latent effects of nursing (Bocherens et al., 2001). These analyses support the others in that Neandertals seemed to prefer large herbivores from open environments, even during warm, forested intervals (Bocherens et al., 2001).

Research continued at several other sites, including Vindija Cave, where evidence of possible Neandertal and anatomically modern human interaction is found. Two Neandertals, dating from 29,000-28,000 years BP were tested, and similar results were reported (Richards

et al., 2000). The $\delta^{13}C$ values for both fauna and Neandertal remains ranged between -21.1 to -19.5 and $\delta^{15}N$ values varied from as low as 1.3 and 1.5 ‰ for the cave bears to 5.2 and 5.3 ‰ for the herbivores to 10.1 and 10.8 ‰ for the Neandertals (Richards et al., 2000). Again, Neandertals were suggested to be top-level carnivores; in this case, Neandertal samples that span from 130,000 to 28,000 years BP all reflect dietary preferences toward large herbivores in open-steppe environments, even during forested or woodland climate conditions (Richards et al., 2000; Bocherens & Drucker, 2003).

Richards et al. (2001) tested nine AMH individuals, including one from Brno-Francouzská and one from Dolni Věstonice in the Czech Republic, two from Kostenki, one from Mal'ta, and three from Sunghir in Russia, and one from Paviland in the United Kingdom. Their $\delta^{13}C$ values all ranged from -19.2 to -18.2 ‰ and the $\delta^{15}N$ values were consistently higher than Neandertals, with the lowest value of 9.3 ‰ and the highest of 15.3‰ (Richards et al., 2001). The authors suggest the elevated values are due to AMH utilizing aquatic resources, such as fish, shellfish, and fowl, and propose this also indicates a broader range of dietary resource exploitation than Neandertals (Richards et al., 2001).

However, this idea was called into question, as isotopic signatures of aquatic resources from this time period, the early Upper Paleolithic, had not been completed (Drucker & Bocherens, 2004). As a result, freshwater fish, eel, and otter remains from two French archaeological sites, Pont d'Ambon and Noyen-sur-Seine, which date to 13,000-9,000 years BP and 8,000 years BP, respectively, were tested for $\delta^{13}C$ and $\delta^{15}N$ values (Drucker & Bocherens, 2004). The $\delta^{13}C$ values ranged considerably, from -24.2 to -16.1 ‰, and the $\delta^{15}N$ values were similarly scattered, with the lowest value of 6.6 ‰ to the highest of 12.3 ‰ (Drucker & Bocherens, 2004). Indeed, the authors used these data to refute the idea of AMH

extensively utilizing aquatic resources in their diet, and suggested that the isotope signatures presented by Richards et al. (2001) can be interpreted as these hominins exploiting large terrestrial herbivores, just like the Neandertals (Drucker & Bocherens, 2004).

Stable isotope analyses of Neandertals have continued, with studies of the Saint-Césaire I Châtelperronian individual (Bocherens & Drucker, 2003; Bocherens et al., 2005). Since few faunal remains are found in the same layer as that Neandertal, comparative faunal remains from La Berbie and Camiac, which date to approximately 35,000 years BP, were used instead (Bocherens & Drucker, 2003; Bocherens et al., 2005). Again, the carbon and nitrogen isotopic signatures indicated a preference toward large herbivores from open environments (Bocherens & Drucker, 2003; Bocherens et al., 2005).

Two additional French Neandertal sites have been examined for stable isotope signatures, with equivalent results (Beauval et al., 2006; Richards et al., 2008). Les-Rochers-de-Villeneuve and Jonzac, which date to 45,000 years BP and 55,000-40,000 years BP, respectively, both show similar $\delta^{13}C$ and $\delta^{15}N$ values to the other Neandertal studies. Specifically, the specimen from Les-Rochers-de-Villeneuve had $\delta^{13}C$ and $\delta^{15}N$ values of -19.0 ‰ and 11.6 ‰, correspondingly (Beauval et al., 2006), and those from Jonzac ranged from -21.3 to -19.7 ‰ and 10.3 to 11.2 ‰ (Richards et al., 2008).

Lastly, Richards and Trinkaus (2009) reviewed the Neandertal and AMH stable isotope data, and included an additional early modern human from Peçstera cu Oase in southwestern Romania, which overlaps with Neandertals, and dates to approximately 40,000 years BP. Of the thirteen Neandertals included in their review (some were excluded from analyses due to collagen preservation problems or subadult status), all specimens recorded $\delta^{13}C$ values less than -19 ‰, indicating that dietary protein was obtained from terrestrial

plants, as marine plants have higher carbon-13 values (Richards & Trinkaus, 2009). Moreover, all the $\delta^{15}N$ values were the expected 3 to 5 ‰ higher than associated herbivore assemblages, and were similar to other carnivores, indicating they were top-level predators, and relied on local large herbivores (Richards & Trinkaus, 2009).

The AMH sample included 14 individuals with carbon values and 10 with both carbon and nitrogen. All specimens date to OIS 3, although the Oase 1 individual is the oldest specimen, and the remainder date between 34,000 years BP and 27,000 years BP (Richards & Trinkaus, 2009). All the AMH samples have $\delta^{13}C$ values of less than -18.5 ‰, which is not significantly different than the average for Neandertals (Richards & Trinkaus, 2009). The $\delta^{15}N$ values are difficult to compare as associated fauna are rare or non-existent; however, faunal assemblages from analogous sites were used, and several of the AMH values were higher than those of Neandertals (Richards & Trinkaus, 2009). For example, the Oase 1 individual had a $\delta^{15}N$ value of 13.3 ‰, and although variation among the AMH sample exists, these elevated levels were attributed to exploitation of aquatic resources (Richards & Trinkaus, 2009).

In summary, the Neandertals examined to date demonstrate a consistency through time and space, with carbon and nitrogen stable isotope analyses indicating a preference toward local herbivores found in open environments (Richards & Trinkaus, 2009). This is strengthened by faunal assemblages at each site, which demonstrate slightly increased $\delta^{13}C$ values and 3 to 5 ‰ increased $\delta^{15}N$ values with each raised tropic level (Richards & Trinkaus, 2009). Additionally, the AMH show similar $\delta^{13}C$ values as Neandertals, which is not surprising given the predominance of C_3 plants in Europe; however, the $\delta^{15}N$ results

show a more varied range of values, with increased numbers potentially indicating the utilization of aquatic fauna (Richards & Trinkaus, 2009).

Direct evidence: dental microwear

Brief History

Dental microwear is the study of microscopic scratches and pits that form on the enamel surface due to the fracture properties of food as a result of food processing and other tooth-use behaviors. This technique has most often been used for dietary reconstruction, although jaw movement patterns, rates of tooth wear, diet and wear correlations, tooth wear agents, and handedness or tool use in food processing have also been investigated (Walker and Teaford 1989).

The earliest dental microwear research used a light microscope to correlate jaw movements to wear facets on molar teeth (Butler, 1952; Mills, 1955; Butler & Mills, 1959), and was then used to determine the wear effect of phytoliths on sheep teeth (Baker et al., 1959). Dahlberg & Kinzey (1962) recognized dental microwear on modern human teeth and correlated the scratch features with food.

These early studies focused on molar teeth; however, the first study to examine dental microwear on incisor teeth was that of Philip Walker in 1976. This research used light microscopy to examine wear striations found on the incisor teeth of Old World monkeys, and correlated striation orientation and frequency with diet and substrate use. Specifically, he found that terrestrial Old World monkeys possessed a greater number of striations than arboreal species, most likely due to an increased exposure to dietary and environmental abrasives. Also, when arboreal forms did demonstrate incisor striations, they were focused on the maxillary central incisors; this was suggested to be due to a low turnover rate in

microwear features (Walker, 1976). Lastly, it was found that the cercopithecines had labiolingual striations in accordance with incisor preparation of dietary resources (Walker, 1976).

These early studies employed light microscopy, which provided investigators with the preliminary data regarding the presence of scratches, pits, and polishes, which could then be linked to diet and behavior (Teaford 2007). While these initial studies were only qualitative in nature, they provided the foundation for what has become dental microwear research. However, there were several technological issues surrounding the use of light microscopy including the limited depth of field and resolving power (Ungar et al., 2008a). It was difficult to collect microwear data across a curved surface, as well as document smaller microwear features (Ungar et al., 2008a).

A resurgence of dental microwear analysis occurred after Walker et al.'s pivotal 1978 SEM-based study on hyraxes and Rensberger's 1978 research on rodent microwear. These studies observed variation in dental microwear between grazers and browsers, and also recorded differences according to seasonality (Rensberger, 1978; Walker et al., 1978). Not only had they proven the effectiveness of microwear research, but they also provided an alternative methodology to light microscopy. For the first time, smaller microwear features were being found and curved surfaces could clearly be seen. This latest method allowed for new questions to be asked, as well as quantitative, rather than just qualitative assessments.

After these initial studies, SEM-based dental microwear research developed extensively, including studies of its utility and methodology (Kathleen Gordon, 1979, 1982; Covert & Kay, 1981; Gordon & Walker, 1983; Kay & Covert, 1983; Ken Gordon, 1984), as well as taphonomic processes that can affect microwear (Teaford, 1988; Teaford & Oyen,

1989a, 1989b; King et al., 1999). The majority of early research focused on extant primate molars to infer fossil hominin dietary preferences or fallback resources, although several studies were devoted to better understanding incisor microwear and how it relates to food preparation, abrasive loads, and non-dietary anterior tooth use behaviors in human and non-human primates, as well as fossil hominins (Ryan, 1979, 1980, 1981; Ryan & Johanson, 1989; Kelley, 1990; Ungar, 1990, 1994a, 1994b, 1996; Ungar & Grine, 1991; Ungar & Spencer, 1999; Ungar et al., 1997; Krueger & Ungar, 2010).

Further studies have led to a more detailed understanding of not only what microwear can indicate in the fossil primate record, but also how microwear forms. Indeed, coupled with the swell of dental microwear research was the recognition of what has been termed the "Last Supper Effect". Microwear defects undergo a turnover rate; that is, new wear features obliterate old ones, and it has been suggested that seasonality of diets can be detected given the short time interval in which individual features form (Walker et al. 1978). Others note that seasonal changes can only be seen in specific environments (Walker and Teaford 1989). Regardless, this turnover rate still leads to the observation of microwear formations of the *past few days or weeks* (Walker and Teaford 1989).

Although the SEM allowed for improved data collection, the process had its own challenges. The microscope was not only expensive to use and maintain, but also could provide erroneous measurements in relation to working distance, contrast differences, and the angle of the specimen (Teaford 1994). The operational mode of the SEM was also a factor to be taken into consideration, as researchers were often limited in the modes their particular SEM possessed. Additionally, SEM research was not standardized; that is, differences between studies ranged from magnification, microwear features identified, and size and

definition of microwear features (Teaford, 2007). For example, one study may describe scratches as being fine, medium, and hypercoarse, while another simply uses the term "scratches" without further categories. One study may describe a scratch as having a 4:1 length-to-width ratio, while another uses a 10:1 ratio. Due to the multiple issues surrounding SEM analysis, new methods were explored.

Although SEM studies continue, there are currently two additional methodological avenues for dental microwear: low-magnification light microscopy and dental microwear texture analysis. One group of researchers returned to light microscopes, using low magnification to determine microwear across an entire tooth. At a magnification of approximately 35X and using a fiber optic light source at a steep angle to the surface, one is able to quickly count microwear features across a much larger area (Semprebon et al. 2004). This is done relatively easily and inexpensively. Moreover, published rates of interobserver error are low, although no error rates of feature category placement between observers has been published (Grine 2007, Teaford 2007, Ungar et al., 2008a).

As with SEM, measurement error is a concern. This not only involves human error, but also the use of a two-dimensional picture to measure a three-dimensional surface (Ungar et al., 2008a). Second, the fiber optic light source angle is extremely important regarding which microwear features are highlighted. Placing the fiber optic light source at one angle makes it easier to see certain microwear features; placing the light sources at a slightly different angle can change the apparent microwear signature drastically. Third, although low-magnification light microscopy is useful for distinguishing broad dietary categories, it does not detect subtle dietary differences, which is especially important in regard to dietary fallback resources (Ungar et al., 2008a).

Thus, another group of researchers went in a different direction. Instead of focusing their efforts on a two-dimensional method, they decided to examine dental microwear in relation to its three-dimensional quality. Thus, dental microwear texture analysis was born (Ungar et al. 2003, 2008a; Scott et al., 2005, 2006).

Dental microwear texture analysis is an objective and repeatable approach to dental microwear, and uses a white-light confocal profiler to create three-dimensional point clouds of dental microwear features (Ungar et al., 2003, 2008a; Scott et al., 2005, 2006). Four adjacent point clouds are created, totaling an area of 204 x 276 μ. Each scan is leveled and any defects, such as preservative, glue, dust, or soil, are removed prior to analyses. The modified point clouds are uploaded to Toothfrax and SFrax scale-sensitive fractal analysis software packages for surface characterization.

There are five texture variables that have shown to be useful when describing dental microwear features: complexity (*Asfc*), anisotropy (*epLsar*), scale of maximum complexity (*Smc*), textural fill volume (*Tfv*), and heterogeneity (*HAsfc*) (Scott et al., 2006, Ungar et al. 2008a). While complexity measures the relief of microwear textures, anisotropy records orientation. Scale of maximum complexity is the steepest point on the complexity plot, and textural fill volume provides texture volume. Lastly, heterogeneity indicates texture variation across the point cloud.

Dental microwear texture analysis has revolutionized microwear practices, and will no doubt become a staple technique in years to come, especially as extant and fossil databases expand. Indeed, this technique has already transcended anthropological boundaries, and is being used more and more in vertebrate paleontology (Ungar et al., 2007). The use of this method in Neandertal and anatomically modern human incisor microwear

research will allow for a dietary and behavioral examination of these hominins of increased resolution and accuracy.

Past Neandertal and AMH dental microwear research

There have been several types of dental microwear research carried out on Neandertal and anatomically modern humans: interproximal, buccal, occlusal, and labial. Interproximal wear describes artificial grooves or striations found at the cemento-enamel junction (CEJ). While they are easily visible and subject to gross examination, researchers use microscopic techniques to infer etiology. One such study observed such grooves on several permanent teeth from the large Neandertal site of Krapina (Frayer & Russell, 1987). Fourteen teeth representing ten individuals demonstrated artificial manipulation on the mesial or distal CEJ, with one lower lateral incisor affected, and the remaining teeth comprised of premolars and molars (Frayer & Russell, 1987). Using a light microscope, the researchers were able to see microstriations and polishes within the groove itself. This led them to suggest these grooves were evidence for early dentistry in the form of toothpick use. Indeed, similar interproximal grooves have been recorded on modern human samples and earlier hominins (Schour & Sarnat, 1942; Kaidonis et al., 1992; Ungar et al., 2001).

The Neandertal mandible from the Spanish site of Banyoles was investigated for interproximal wear (Lalueza et al., 1993). An artificial groove was located at the CEJ between the M_2 and M_3, and upon SEM examination, was found to be polished with small striations on the interior surface (Lalueza et al., 1993). Experimental data provided additional evidence that this groove could have been caused by toothpick use (Lalueza et al., 1993).

Artificial, subvertical grooves have also been reported for Neandertal posterior and anterior dental remains at several sites, including El Sidrón in Spain and Figueira Brava in Portugal (Egocheaga et al., 2004; Estalrrich et al., 2011). Some indicated the etiology was a combined consequence of abrasive diets requiring a high bite force (Egocheaga et al., 2004). More specifically, the subvertical grooves could have formed as a compensatory mechanism to maintain posterior teeth in their occlusal-cervical position during the biomechanical stress that accompanies the mastication of hard plant foods (Egocheaga et al., 2004). The enamel prism orientation in the mesial and distal interproximal areas are suggested by the authors to favor this interpretation (Egocheaga et al., 2004).

Recent analyses of a larger sample of Neandertal teeth from El Sidón do not support this interpretation (Estalrrich et al., 2011). This study found subvertical grooves on 60/93 (64.5%) teeth. While all tooth types were affected, the grooves were most often found on the posterior teeth. They refute the ideas that biomechanical stress or enamel prism organization played a role in the etiology, but rather, suggest that the cause could be dietary or paramasticatory. Further analyses are required (Estalrrich et al., 2011).

Several buccal microwear analyses have also been completed, and these studies focus on microwear features, most often striations or scratches, found on the buccal sides of posterior teeth (Lalueza Fox & Pérez-Pérez, 1993; Lalueza et al., 1993,1996; Pérez-Pérez et al., 2003). Studies of buccal microwear began in the late 1980's when it was suggested that striation length and orientation could indicate the amount of meat and plant dietary resources (Pérez-Pérez, 2004). Although these associations are more complex than originally thought, with striation density being the most distinguishing variable, differences between and within modern human samples have been documented (Pérez-Pérez, 2004). The most important

implication is that more meat-reliant populations, such as those from the arctic, display few and short striations, whereas those reliant on plant resources show the opposite pattern (Pérez-Pérez, 2004). This is proposed to be due to differences in dietary and/or environmental abrasive loads.

Buccal microwear researchers propose that this method is less affected by "Last Supper Effect" of occlusal microwear; that is, the turnover rate is considerably slower (Pérez-Pérez, 2004). However, challenges correlating striation patterns with cultural and environmental conditions have presented themselves, although some strides have been made (Pérez-Pérez et al., 2003). It is, for example, unclear exactly how microwear forms on buccal surfaces, since these are likely not used in chewing.

Early buccal microwear studies focused on a small sample of Neandertal individuals, and used light or scanning electron microscopy to document striation density and orientation. The light-microscopy based analysis of the Banyoles mandible found a high number of striations, suggesting this Neandertal relied on a mixed, plant-based, and abrasive diet (Lalueza et al., 1993). This interpretation was based on results for modern human comparative groups with similar abrasive loads and dietary preferences, namely Andaman Islanders and Australian aboriginals, that showed a similar signal (Lalueza et al., 1993). Buccal analyses of the Gibraltar 2 child from Devil's Tower suggested a more abrasive diet than that of a medieval subadult comparative sample that relied on a mixed diet, with an emphasis on plant resources. Although the striation density was higher than that found on meat-eating samples (Greenland Inuit and Fuegians), this child was suggested to have relied heavily on meat (Lalueza & Pérez-Pérez, 1993).

Expanded buccal microwear analyses have since been completed, including larger samples of Middle and Upper Paleolithic hominins (Lalueza et al., 1996; Pérez-Pérez et al., 2003). The first study examined 20 fossil hominins and compared them to several modern human samples of varying diets (Lalueza et al., 1996). This SEM-based study found that while variation existed in both fossil groups, Neandertal buccal microwear patterns were most congruent with the meat-eating modern human samples, namely, Greenland Inuit, which suggests hunting strategies ((Lalueza et al., 1996). On the other hand, many of the Upper Paleolithic fossils demonstrated a more abrasive diet, indicating more reliance on plant-based strategies (Lalueza et al., 1996).

Another study examined 68 fossil humans from Western Eurasia (Pérez-Pérez et al., 2003). The buccal microwear signature of the Neandertal sample was heterogeneous, with striation length, density, and orientation variables spanning a wide range of values. This was inconsistent with the generally held belief that Neandertals were mainly carnivorous, as suggested by faunal assemblages and stable isotope analyses. Instead, it was proposed that Neandertals relied on a mixed diet of both plant and animal resources; in fact, when climate was accounted for, the signatures demonstrated a clearer pattern (Pérez-Pérez et al., 2003). An increase in striations appeared in colder climates, whereas the density decreased during warm periods (Pérez-Pérez et al., 2003). The authors suggest this was due to an increase in plant intake during cold conditions and animal reliance at warmer intervals; however, this seems counterintuitive when issues of plant accessibility and availability are considered.

Occlusal microwear research using dental microwear texture analysis has demonstrated some indications of differences within the Neandertals, as well as between Neandertals and early Upper Paleolithic hominins (El Zaatari, 2007). Statistical analyses

were limited due to sample size; however, differences were suggested between the European cold, open steppe and warm, woodland sites. Specifically, European Neandertals that lived in open steppe environments had lower complexity values than those associated with woodland conditions (El Zaatari, 2007). This was interpreted as indicating an increase in abrasive loads associated with a wider plant resource base for the woodland Neandertals (El Zaatari, 2007). On the other hand, the low complexity values of the cold, open steppe individuals were suggested to indicate an increased reliance on meat resources. Indeed, this fossil subgroup was closest in complexity values to those of the Fuegians, a sample population reliant upon meat resources (and also included in this dissertation).

Those in European woodland environments varied within themselves, and those sites with coniferous forest and Mediterranean evergreen forest had less complexity than those sites with deciduous forest (El Zaatari, 2007). The greater complexity values of the deciduous forest sites were suggested to indicate higher dietary abrasive loads than the other two woodland environments. Indeed, the increase in complexity values from open steppe to coniferous and Mediterranean evergreen to deciduous forests was interpreted as an increase in abrasive diets (El Zaatari, 2007).

The Levantine Neandertals were examined separately, and due to the small sample size, no statistical analyses were possible. However, the Amud 1 Neandertal had a microwear signature similar to that found for the European deciduous forest sample, and the Kebara 2 signal was close to that of the European coniferous forest subgroup (El Zaatari, 2007). The two individuals from Tabūn, 1 and 2, were most similar in microwear textures to the European Neandertals from deciduous and coniferous environments, respectively (El

Zaatari, 2007). It was suggested that the microwear signatures of the Levantine Neandertals indicate these individuals' diets were not exclusively composed of meat (El Zaatari, 2007).

The early Upper Paleolithic sample had a wider range of complexity values, which was interpreted as being reflective of their dietary breadth (El Zaatari, 2007). However, these values were not significantly different from those of northern and central European Neandertals, but were significantly different from southern European Neandertals (El Zaatari, 2007). This difference was interpreted as indicating a more diverse diet for southern European Neandertals, which correlates well with faunal assemblages (El Zaatari, 2007).

The final type of microwear analyses are labial, or those investigating the labial surface of anterior teeth. Several Neandertal dental studies have questioned the etiology of the excessive wear of the anterior teeth, which, in its extreme, demonstrates labial-lingual rounding. Although several ideas have been proposed, as described above, the most common is the use of the anterior dentition as a clamp, tool, or third hand. This was inferred by analogy from ethnographic reports of Alaskan Eskimo and Canadian and Greenland Inuit populations using their front teeth in this manner.

The first microwear analysis of European and Levantine Neandertal anterior teeth was an SEM-based study that used non-human (common chimpanzees, gorillas, and baboons) and human (Ipiutak from Point Hope, Alaska and Native American aboriginals from the Libben Site in Ohio) comparative samples to infer Neandertal behavioral strategies (Ryan, 1980). This study defined microwear features as small, large, and patches of pits, as well as fine scratches, gouges, and polishing. Incisal edge damage, such as microflaking and concentrated patches of pits were also recorded (Ryan, 1980).

The non-human primates demonstrated microwear patterns consistent with diet and feeding behaviors. The gorilla sample had labial-lingual striations, polishing, and small pits, interpreted as a result of their feeding behaviors in which pith or leaves are stripped from stems or trees (Ryan, 1980). The chimpanzee sample had the same three microwear features, but the striations were oriented more mesial-distally and there was a high frequency of pitting on the labial surface. The chimpanzee microwear signature was attributed to the use of the incisors for slicing into fruits, and also stripping leaves from terminal branches (Ryan, 1980). The desert baboon sample demonstrated wear striations, pitting, and polishing, but most notably had high rates of incisor edge damage in the form of enamel and dentine microflaking and central and lingual incisor wear. This pattern was interpreted as a result of grit adherent on tough foods such as roots and seeds (Ryan, 1980).

The human comparative sample also demonstrated incisor microwear signals. The Libben sample was examined by age group, with both deciduous and permanent incisors analyzed. Not surprising, an overall increase in enamel wear and dentine exposure occurred through time (Ryan, 1980). Moreover, pits, patches of pits, fine wear striations, and flaking were all found on the specimens, and were attributed to the use of mortars and pestles introducing dietary and environmental abrasives in the diet and an occasional use of the incisors in non-dietary anterior tooth use behaviors (Ryan, 1980).

The Ipiutak sample from Point Hope (used in this dissertation as well), had a different microwear signal. Indeed, 70% this sample displayed large flaking areas, defined as gouges, and microflakes, pits, patches of pits, and fine wear striations were also recorded (Ryan, 1980). The Ipiutak relied on a heavy regimen of non-dietary anterior tooth use behaviors, such as intense grasping and clamping activities in relation to hide preparation for clothing

production. This intense regimen, along with a grit-laden diet of meat, was given as the cause of the microwear signal (Ryan, 1980).

Neandertal microwear features varied among the sample, but nearly all individuals had a high incidence of gouging features. Microflaking, large pitting, and fine wear striations were also found on specimens (Ryan, 1980). The overall microwear signal of these Neandertal individuals was suggested to reflect continuous contact with abrasive materials, and most closely resembled those of the Ipiutak sample from Point Hope (Ryan, 1980). Ryan (1980) attributed the similar signals of the Ipiutak and Neandertals as both samples participating in power-grasping and clamping activities of the anterior dentition. This strengthened the association between Neandertals, arctic populations, and non-dietary anterior tooth use behaviors (Ryan, 1980).

Labial striations were also examined on the large dental sample from Krapina (Lalueza Fox & Frayer, 1997). This study found two types of scratches: 1. those on the labial surface, closest to the incisal edge, that were indicative of grasping abrasive materials in between the front teeth and 2. those on the central labial surface that signified cutting marks from stone tools (Lalueza Fox & Frayer, 1997). The latter type buttressed the idea of the "stuff and cut" scenario, in which Neandertals would hold a piece of meat in between their anterior teeth and cut a portion of it close to their lips. Additionally, dental microwear texture analysis of the Krapina Neandertals supported the former type, with high heterogeneity values and low anisotropy values, indicating high abrasive loads and non-dietary anterior tooth use behaviors, respectively (Krueger & Ungar, in preparation).

As mentioned above, the large striations found on the central labial surfaces of anterior teeth have been described as indicative of the "stuff and cut" method. The

hypothesis suggests the Neandertals would, at times, inadvertently drag their stone tool across the labial surface of the anterior teeth, creating large gouges. The idea of examining the gouge orientation for indications of handedness was suggested; however, striation orientations of several modern human comparative samples, including Aleut, Arikara, Illinois Bluff, and Puye Pueblo, did not demonstrate diagonal striation patterns indicative of handedness (Bax & Ungar, 1999).

Overall, the past dental microwear analyses have focused on animal and plant dietary resources, dietary and environmental abrasive loads, and non-dietary anterior tooth use behaviors, especially as they relate to arctic populations. However, the majority of these studies have utilized light or scanning election microscopy, which are both plagued by methodological challenges. Moreover, important variables, such as paleoclimate reconstructions, time interval, site location, and indirect and direct forms of dietary reconstruction have not been integrated into interpretive models. This study will not only use an objective, repeatable, and three-dimensional method for the collection and characterization of dental microwear, but will also interpret these data to provide a synthesis of Neandertal and anatomically modern human dietary and behavioral strategies.

CHAPTER THREE: MATERIALS & METHODS

A total of 378 anterior teeth are used in this study, comprised of 69 Neandertal, 52 anatomically modern human, and 257 modern human comparative individuals. Of the Neandertal sample, four individuals are represented by deciduous teeth and 65 by their permanent dentition. The anatomically modern human sample has 10 individuals with deciduous teeth and 42 with permanent teeth. All the modern human comparative individuals are represented by permanent maxillary central incisors. While data are reported for the deciduous teeth, they are not compared in statistical analyses with data for permanent teeth given implications of differences in degree of mineralization and tooth hardness for microwear formation.

The Neandertal sample ranges in time from OIS 7 to OIS 3, and includes individuals from 30 sites in 11 countries across Western Eurasia. The countries included, along with the number of sites in parentheses, are Belgium (2), Croatia (2), Czech Republic (2), France (15), Gibraltar (1), Great Britain (1), Hungary (1), Italy (1), Spain (1), Iraq (1), and Israel (3) (Fig. 3.1). The anatomically modern human sample dates to OIS 3 and 2, and includes 16 sites from five countries across Western Eurasia. This countries included, along with the number of sites in parenthesis, are Croatia (1), Czech Republic (2), France (9), Italy (1), and Israel (3) (Fig. 3.2).

The modern human comparative baseline samples extend from 5000 BP to the early 20th century. These 13 samples include five from a previous publication (Krueger and Ungar, 2010), along with eight new ones. The comparative samples include: Aleut (n=24), New Kingdom Egyptians from Amarna (n=14), Andamanese (n=15), Arikara (n=18), Chinese immigrants (n=16), Chumash (n=19), Fuegians (n=5), Illinois Bluff (n=20), Nunavut

Sadlermiut (n=27), Point Hope, Alaska [Ipiutak (n=22) and Tigara (n=34)], Prince Rupert Harbour Tsimshian (n=25), and Puye Pueblo (n=18) (Fig. 3.3). A more detailed description of each comparative sample is found below.

Each fossil site has its own excavation history, and in an attempt to standardize information, consistent metadata were used to put each site into comparative context. First, a description of the location of each site is provided, including the nearest modern-day city, mountain range, latitude, and water source. This is to help provide a range of geographic information, including global, regional, and local. The water source information is particularly helpful when interpreting whether a site is interior or coastal, as differences in subsistence strategies have been suggested to exist between these two broad categories. Second, lithic and faunal assemblages are listed in an attempt to understand the local stone tool industry among the sites with the former, as well as to better correlate predicted climate conditions with the latter. Third, an approximate range of dates, along with its associated marine oxygen isotope stage (OIS or MIS) is given, as well as climate reconstruction and the sources from which these datasets were taken. Last, specific stratigraphic information for individual fossil specimens used in this study is provided, along with the particular tooth used, and miscellaneous information, such as stable isotope analyses and unique site records pertinent to this study. While some sites have extensively detailed field notes, others do not. Therefore, some sites will have considerably more information than others; however, this imbalance was overlooked in order to provide as much data as possible not only for this study, but also for future research as well.

Figure 3.1: Map showing Neandertal sites used in this study.

The fossil sample: Neandertals

Belgium

Engis

Site Information

Location: Awirs Cave, north of Engis, Belgium

Latitude: 50° 36' 0" N

Interior or coastal site: Interior, near the Meuse River

Lithic Industry: Mousterian

Faunal Assemblage: Woolly rhinoceros, reindeer, woolly mammoth

Date: OIS 3: 40,000 to 35,000 years BP, based on associated fauna

Climate: Cool, open tundra

Sources: Fraipont, 1936; Cordy, 1988; Schwartz & Tattersall, 2002

Specimen information

Four maxillary deciduous teeth from the Engis 2 Neandertal were examined for dental microwear. The right and left canines did not preserve microwear, while the upper left lateral and right central incisors preserved antemortem wear. The Rdi^1 was selected for scanning. The Engis 2 Neandertal is a subadult, and estimated to be approximately 3 to 4 years old (Schwartz & Tattersall, 2002). In addition, this specimen has been tested for stable isotope values, and has $\delta^{13}C$ and $\delta^{15}N$ values of -19.6 and 12.6 ‰, respectively (Bocherens et al., 2001). High-resolution dental casts were provided by Prof. Jean-Jacques Hublin at the Max Planck Institute for Evolutionary Anthropology.

Scladina

Site Information

Location: Scladina Cave, near Sclayn, Belgium

Latitude: 50° 29' 0" N

Interior or coastal site: Interior, near the Meuse River

Lithic Industry: Mousterian

Faunal Assemblage: Horse, fallow deer, cave bear, wild boar, badger, red and arctic fox, cave lion, cave hyena, and wolf

Date: OIS 5e: 127,000 years BP (gamma spectrometry), 110,000 years BP ($^{230}Th/^{234}U$), 100,000 years BP (thermoluminescence) or 5a: 80,000 years BP (palynology and micropaleontology)

Climate: Temperate and forested

Sources: Cordy, 1988; Bocherens et al., 1999, 2001; Schwartz & Tattersall, 2002

Specimen information

One Neandertal subadult, estimated to be 8 years old, was located in sublevel 4A, and eight permanent teeth were examined for antemortem microwear. All eight preserved microwear of varying quality, including the mandibular right canine and lateral incisor and maxillary right and left canines, right and left lateral incisors, and right central incisor. The RC_1 was selected for analyses because of the pristine quality of the microwear signature. Stable isotopes of this individual show $\delta^{13}C$ and $\delta^{15}N$ values of -19.9 and 10.9 ‰, respectively (Bocherens et al., 1999). High-resolution dental casts were provided by Prof. Jean-Jacques Hublin at the Max Planck Institute for Evolutionary Anthropology.

Croatia

Krapina

Site Information

Location: Rockshelter site in Krapina, Croatia

Latitude: 46° 10' 0" N

Interior or coastal site: Interior, near the Krapinčica River

Lithic Industry: Mousterian of Charentian type

Faunal Assemblage: Merck's rhinoceros, bison, auroch, giant deer, cave bear, brown bear, horse, beaver, and Neandertals (with cutmarks)

Date: OIS 6 to 5e: 130,000 years BP (ESR dating)

Climate: Temperate forest

Sources: Osborn, 1915; Rink et al., 1995; Simek & Smith, 1997; Schwartz & Tattersall, 2002; Karavanić, 2004

Specimen information

The hominin collection from Krapina represents the largest Neandertal sample found to date, with 874 individual elements, including 281 teeth or tooth fragments (Simek & Smith, 1997; Karavanić, 2004; Frayer, personal communication). The majority of the remains were excavated from levels three to four, often referred to as the "Hominid Zone", and five to seven; however, the levels accumulated quickly, and all the hominins may be considered penecontemporaneous (Schwartz & Tattersall, 2002).

Forty-three permanent anterior teeth representing seventeen individuals were analyzed for dental microwear, and the tooth with the most pristine surface was selected to represent each Krapina Dental Person (KDP). High-resolution dental casts of the Krapina collection were provided by Prof. David Frayer of the University of Kansas and Drs. Luca Bondioli and Ivana Fiore of the Museo Nazionale Preistorico Etnografico "L. Pigorini" Sezione di Antropologia.

Vindija

Site Information

Location: Vindija cave, near Donja Voća, Croatia

Latitude: 46° 18' 0" N

Interior or coastal site: Interior, near the Drava River

Lithic Industry: Layer G_3 is late Mousterian, layer G_1 is a mixture of Mousterian and Upper Paleolithic, and F-C are Upper Paleolithic

Faunal Assemblage: G complex: Roe deer, cave bear, cave lion, wolf

Date: Level G_3: OIS 3: 42,000 years BP (AMS and amino-acid racemization)

Level G_1: OIS 3: 30,000 to 28,000 years BP (AMS)

Climate: G complex: Temperate woodland/forest

Sources: Wolpoff et al., 1981; Smith et al., 1985; Krings et al., 2000; Schwartz & Tattersall, 2002; Ahern et al., 2004; Karavanić, 2004; Janković et al., 2006

Specimen information

Vindija Cave has been excavated intermittently since the 1970s, and the discovery of both Neandertal and anatomically modern human remains, along with a unique mixture of lithic assemblages, has been the subject of several debates (Karavanić & Smith, 1998, 2000; d'Errico et al., 1998; Ahern et al., 2004; see Chapter 2). Although there are 13 stratigraphic layers (A through M), the most controversial has been the five sub-units of level G (Janković et al., 2006). The oldest, G_3, has yielded the majority of the Neandertal specimens, which were found in association with Mousterian tools (Ahern et al., 2004). The more recent G_1 layer also has Neandertal remains, but with a mixture of Mousterian and Upper Paleolithic tools (Ahern et al., 2004). Subsequently, the F and D layers transition into modern human remains and Upper Paleolithic tools (Ahern et al., 2004). This mixture of tool traditions in the G_1 layer has sparked debate about the possible imitation of or trade with modern humans (Karavanić & Smith, 1998, 2000). Moreover, supporters of multiregional evolution recognize this site as evidence of a direct transition from Neandertals to modern humans; however, cryoturbation is a significant problem in the cave, and this interpretation has been criticized (Karavanić & Smith, 1998, 2000; d'Errico et al., 1998). Two Neandertal specimens from the G_1 layer were analyzed for stable isotopes and their $\delta^{13}C$ and $\delta^{15}N$ values were: (Vi-207) -19.5 and 10.1, ‰ and (Vi-208) -20.5 and 10.8 ‰, respectively (Richards et al., 2000).

Four permanent Neandertal teeth from the controversial G layers were analyzed for dental microwear, and all four preserved, antemortem wear. These four individuals and their

tooth type are: Vi 12.2 (RI_2), Vi 12.3 (RI^2), Vi 12.7 (LI_2), and Vi 290 (RI^1). The specimen numbers are currently undergoing a transition, with the 12.X numbers indicating the new system and Vi 290 still maintaining the old method (Wolpoff et al., 1981; Ahern et al., 2004). The 12 indicates a hominin dental remain, and the number proceeding the decimal point indicates the tooth number (Ahern et al., 2004). High-resolution dental casts of these specimens were provided by Profs. Alejandro Pèrez-Pèrez and David Frayer.

Czech Republic

Kůlna

Site Information

Location: Kůlna Cave near Sloup Village, Czech Republic

Latitude: 49° 25' 0" N

Interior or coastal site: Interior, near the Punkva River

Lithic Industry: Level 7a: Mousterian of Micoque tradition

Faunal Assemblage: Level 7a: Reindeer, woolly mammoth, woolly rhinoceros, moose, and horse

Date: OIS 3 : 45,000 to 40,000 years BP (ESR and C-14)

Climate: Cold, steppe conditions

Sources: Oakley et al., 1971; Rink et al., 1996; Schwartz & Tattersall, 2002

Specimen information

The maxillary right canine of the Kůlna 1 adult, found in level 7a, was available and preserved antemortem dental microwear. High-resolution dental casts were provided by Prof. Jean-Jacques Hublin.

Ochoz

Site Information

Location: Schwedentischgrotte or Sveduv Stul or Ochozská Cave near Ochoz, Czech Republic

Latitude: 49° 20' 0" N

Interior or coastal site: Interior, near the Svitava River

Lithic Industry: Mousterian of Eastern tradition

Faunal Assemblage: Early Würm fauna (OIS 4) (no specific names listed)

Date: Stratigraphic location of the Ochoz 1 mandible is unknown, but most likely dates to OIS 5.

Climate: Unknown

Sources: Vlček, 1969; Schwartz & Tattersall, 2002

Specimen information

The Ochoz 1 mandible was found in 1905, and the stratigraphic context is between one of two similar strata composed of reddish clay (Schwartz & Tattersall, 2002). Four mandibular anterior teeth, the left canine, lateral incisor, and central incisor, as well as the right central incisor, were examined for antemortem microwear. All four demonstrated wear, and the LI_2 was selected to represent the individual based on the quality of the microwear. High-resolution dental casts were provided by Prof. Jean-Jacques Hublin.

France

Arcy-sur-Cure

Site Information

Location: Grotte de l'Hyène of the Arcy-sur-Cure cave system near Auxerre, France

Latitude: 47° 35' 0" N

Interior or coastal site: Interior, near the Cure River

Lithic Industry: Denticulate Mousterian

Faunal Assemblage: Horse, woolly rhinoceros, reindeer, chamois, woolly mammoth

Date: OIS 4

Climate: Faunal assemblages suggest cold, open tundra in OIS 4

Sources: Leroi-Gourhan, 1958, 1961; Leroi-Gourhan & Leroi-Gourhan, 1964; Farizy, 1990; Mellars, 1996; Frayer et al., 2006

Specimen information

Three Neandertal specimens, Arcy-sur-Cure 8 (Arcy II) and 9 (Arcy III) and Arcy D4 IVb^6 (D4 designates location on the grid system, IVb^6 designates the sixth stratum of the IVb horizon, Leroi-Gourhan, 1958) were available for study, including the mandibular right canine through left lateral incisor of Arcy 8 (Arcy II), the maxillary left central and right lateral incisors of Arcy 9, and the maxillary left lateral incisor of Arcy D4 IVb6.

All three of these individuals were located in layer 20 of the Grotte de l'Hyène, which is part of the Arcy-sur-Cure cave systems (Leroi-Gourhan, 1958, 1961). These specimens were first described in Leroi-Gourhan, 1958, and are listed as 1, 2, and 6 on page 113 in that paper. Only Arcy 8 and 9 preserved , unobscured antemortem microwear. High-resolution casts of these individuals were provided by Profs. Jean-Jacques Hublin and Erik Trinkaus.

Biache-Saint-Vaast

Site Information

Location: River terrace site halfway between Arras and Douai, France

Latitude: 50° 18' 0" N

Interior or coastal site: Interior, near the Scarpe River

Lithic Industry: Mousterian of Ferrassie type (early Neandertal)

Faunal Assemblage: Bear (evidence of hunting), Merck's rhinoceros, red, roe, fallow deer, auroch

Date: OIS 7-6: 245,000 to 175,000 years BP (pollen, fauna, and thermoluminence)

Climate: Temperate forest

Sources: Auguste, 1988; Schwartz & Tattersall, 2002; Rougier, 2003

Specimen information

The Biache-Saint-Vaast 1 individual was excavated in 1976, and an isolated maxillary incisor was available for analysis. Microwear textures were preserved on this tooth, and the high-resolution cast was provided by Prof. Jean-Jacques Hublin.

Combe Grenal

Site Information

Location: Combe-Grenal cave near Domme, France

Latitude: 44° 48' 0" N

Interior or coastal site: Interior, near the Dordogne River

Lithic Industry: Charentian Mousterian of La Quina type

Faunal Assemblage: Reindeer, horse, woolly mammoth, woolly rhinoceros

Date: OIS 4: 70,000 years BP

Climate: Cold and dry, with pollen suggesting only pine survived

Sources: Auguste, 1988; Mellars, 1996; Garralda & Vandermeersch, 2000; Schwartz & Tattersall, 2002; Rougier, 2003

Specimen information

The site of Combe-Grenal was excavated extensively by François Bordes from 1953 to 1965, and the stratigraphic sequence is especially significant as it spans from OIS 6 through 3 (Mellars, 1996). Due to its unique, continuous sequence, faunal and lithic assemblages, pollen sequences, and sediment studies have been rigorously examined to better understand change in Neandertal behavior over time and variation by climate (Mellars, 1996).

The vast majority of the Neandertal specimens come from layer 25 (Bordes' layer N), and two anterior teeth, the maxillary left central incisor of F4-742 (Combe-Grenal V) and a maxillary right central incisor of E2-133 (Combe-Grenal XI) was scanned for antemortem microwear (Garralda & Vandermeersch, 2000). High-resolution casts were provided by Prof. Erik Trinkaus.

La Chaise-de-Vouthon: Abri Suard

Site Information

Location: Suard rock shelter near Vouthon, France

Latitude: 45° 40' 0" N

Interior or coastal site: Interior, near the Tardoire River

Lithic Industry: Upper Acheulean tradition (early Neandertal)

Faunal Assemblage: Bovids, horse

Date: OIS 7/6: 200,000 to 175,000 years BP (Th/U, thermoluminescence)

Climate: Warm, humid, and wet, with pollen suggesting pine, fir, hazel, and willow

Sources: David & Prat, 1965; David et al., 1965; Legoux, 1976; Blackwell et al., 1983

Specimen information

Two isolated permanent anterior teeth were available for microwear analysis, and both preserved microwear signatures. The first, S33, is a maxillary right lateral incisor that was located in layer 53. The second, S41, is a maxillary left central incisor, and was located in layer 54, with the majority of remains. Both layers date to OIS 7. High-resolution dental casts of these specimens were provided by Prof. Jean-Jacques Hublin at the Max Planck Institute for Evolutionary Anthropology.

La Chaise-de-Vouthon: Abri Bourgeois-Delaunay

Site Information

Location: Bourgeois-Delaunay rock shelter near Vouthon, France

Latitude: 45° 40' 0" N

Interior or coastal site: Interior, near the Tardoire River

Lithic Industry: Upper Acheulean tradition

Faunal Assemblage: Horse, roe dear, red deer, rhinoceros, bovid, cave bear, wolf, fox, hyena

Date: OIS 6/5e: 150,000 to 120,000 years BP (Th/U); 128,000 years BP (speleothem)

Climate: Warm and temperate with deciduous forest, with pollen suggesting oak, elm, hazel, linden, birch, and alder.

Sources: David & Prat, 1965; Oakley et al., 1971; Blackwell et al., 1983; Rae & Ivanovich, 1986; Condemi, 2001; Couchoud et al., 2009

Specimen information

Eleven specimens from the contemporaneous layers 11 and 12 were analyzed for dental microwear. Those from layer 11 are: BD 10 (LI^2), BD 11 (RC^1), BD 12 (LI^1), BD 13

(LC_1), BD 15 (RC^1), BD 16 (RC^1), BD 19 (Rdc_1), BD 20 (LI_1), and BD 21 (RI_1). Those from layer 12 are BD A (RI_2) and BD B (LC_1). All but BD A preserved antemortem microwear. High-resolution casts were provided by Prof. Jean-Jacques Hublin.

La Ferrassie

Site Information

Location: La Ferrassie rock shelter

Latitude: 44° 57' 0" N

Interior or coastal site: Interior, near the Vézère River

Lithic Industry: Charentian Mousterian of La Ferrassie type

Faunal Assemblage: Horse, woolly rhinoceros, wild boar, red deer, reindeer, wolf, hyena, cave bear, and fox

Date: OIS 4: 70,000 to 60,000 years BP

Climate: Cool and dry

Sources: Mellars, 1996; Schwartz & Tattersall, 2002

Specimen information

Two specimens were examined for dental microwear textures. These were the famous La Ferrassie I and II specimens, an adult male and adult female, respectively. These are well-known individuals not only for the excessive wear of the anterior teeth, but also as indication of burial in Neandertal society (Mellars, 1996). Four maxillary anterior teeth of La Ferrassie I were scanned for dental microwear: the left and right central incisors, right lateral incisor, and right canine. The lack of enamel resulted in only the maxillary right central incisor preserving antemortem microwear. Three maxillary anterior teeth of La Ferrassie II were analyzed, including the right canine, lateral incisor, and central incisor. The

right lateral incisor was selected for analysis. High-resolution replicas of these teeth were provided by Prof. Jean-Jacques Hublin.

La Quina

Site Information

Location: Rock shelter close to Villebois-Lavalette, France

Latitude: 45° 30' 0" N

Interior or coastal site: Interior, near the Voultron River

Lithic Industry: Mousterian of the Quina type

Faunal Assemblage: Reindeer, horse, steppe bison, auroch, mammoth

Date: OIS 4-3: 65,000 to 35,000 years BP

Climate: Cold to moderate open steppe conditions

Sources: Mellars, 1996; Schwartz & Tattersall, 2002; Hardy, 2004

Specimen information

Three permanent, anterior teeth from La Quina 5 (maxillary right and left lateral incisors, right central incisor) and the lower left canine from La Quina 17 were available for microwear analyses. While all three teeth from La Quina 5 preserved microwear, no microwear preserved on the labial surface of La Quina 17. The maxillary right lateral incisor from La Quina 5, an adult female, was included in the analyses due to the pristine quality of the microwear features. High-resolution casts were provided by Profs. Jean-Jacques Hublin and Erik Trinkaus.

Le Moustier

Site Information

Location: Rock shelter near Le Moustier, France

Latitude: 45° 00' 0" N

Interior or coastal site: Interior, near the Vézère River

Lithic Industry: Typical Mousterian

Faunal Assemblage: Horse, reindeer

Date: OIS 3: 40,000 years BP (thermoluminescence and ESR dating)

Climate: Cold and open conditions, with only pine represented in the arboreal pollen sequence

Sources: Mellars, 1996; Schwartz & Tattersall, 2002

Specimen information

Le Moustier was excavated in 1908 by Otto Hauser, and two Neandertal individuals, LM 1 and LM 2, were located in Bed J and H-I, respectively (Schwartz & Tattersall, 2002). The LM 1 specimen represents a subadult of 15 to 18 years of age, and LM 2, an infant, was lost prior to being examined (Schwartz & Tattersall, 2002). Three permanent anterior teeth from LM 1 were available for microwear analysis, including the maxillary right central and lateral incisors and the mandibular left lateral incisor. Both the maxillary incisors demonstrated pristine microwear surfaces, and the right central incisor was selected for analysis. High-resolution dental casts were provided by Prof. Alejandro Pérez-Pérez.

Le Petit-Puymoyen

Site Information

Location: Cave near Puymoyen, France

Latitude: 45° 37' 0" N

Interior or coastal site: Interior, near the Eaux-Claires River

Lithic Industry: Mousterian of La Quina type

Faunal Assemblage: Reindeer, auroch, horse, wolf, fox

Date: OIS 3: 50,000 years BP

Climate: Cold, open conditions

Sources: Guillien, 1961, 1965; Oakey et al., 1971; Granat & Peyre, 2010

Specimen information

One specimen from Le Petit-Puymoyen, found in January 1908 by A. Favraud, was available for analysis. The specimen PPm 3, represented by a mandibular right canine, preserved clean, antemortem dental microwear. The cast was provided by Prof. Jean-Jacques Hublin.

Les Pradelles (Marillac)

Site Information

Location: Les Pradelles cave system near Marillac-le-Franc

Latitude: 45° 44' 0" N

Interior or coastal site: Interior, near the Ligogne River (tributary of the Tardoire).

Lithic Industry: Mousterian of the La Quina type

Faunal Assemblage: Dominated by reindeer, prompting some to suggest the site represents a reindeer hunting camp. Horse and bison are also present.

Date: OIS 3: 45,000 to 40,000 years BP

Climate: Sediment and faunal assemblages suggest cold, open, steppe environment

Sources: Bocherens et al., 1991; Fizet et al., 1995; Costamagno et al., 2006

Specimen information

Five unnumbered maxillary adult teeth, located in layers 9 or 10 (of 12 total stratigraphic horizons), were scanned for dental microwear, including all anterior teeth

except the left canine. As a result of the unnumbered status, as well as the lack of duplication in tooth type, these teeth were considered one individual, and only the LI^1 was selected for analyses. High-resolution casts of these teeth were provided by Prof. Jean-Jacques Hublin at the Max Planck Institute for Evolutionary Anthropology.

Monsempron

Site Information

Location: Cave near Monsempron-Libos, France

Latitude: 44° 29' 0" N

Interior or coastal site: Interior, near the Lot River

Lithic Industry: Charentian Mousterian of the La Quina type

Faunal Assemblage: Horse, reindeer, auroch, bison, wolf, fox, hyena

Date: OIS 4: 71,000 to 57,000 years BP

Climate: Cold, open steppe

Sources: Coulonges et al., 1952; Condemi et al., 2010

Specimen information

Four unnumbered teeth, including three maxillary (right canine, lateral and central incisors) and one mandibular left canine were available for microwear analyses, and all but the RC^1 preserved wear. Descriptions of the teeth suggest the LC_1 is from mandible *b*, and the RC^1 and RI^2 are from maxilla *h*; however, the RI^1 is not described specifically, but could be the isolated LI^1 labeled *c* (Coulonges et al., 1952). Therefore, three individuals could be represented in the four teeth, but because this is unconfirmed, the LC_1 and RI^1 were selected for analysis. Dental casts were provided by Prof. Jean-Jacques Hublin.

Moula Guercy

Site Information

Location: Moula-Guercy cave in Ardèche

Latitude: 44° 45' 0" N

Interior or coastal site: Interior, near the Rhone River

Lithic Industry: Mousterian of Ferrassie type

Faunal Assemblage: Red deer, wild goat, Neandertals (with cutmarks)

Date: OIS 5: 120,000 to 100,000 years BP

Climate: Temperate forest

Sources: DeFleur et al., 1999

Specimen information

The Moula-Guercy cave has yielded several Neandertal fossils, all from layer XV, which dates to 120,000 to 100,000 years BP. Four permanent anterior teeth, representing four Neandertal individuals, were available for study, and all preserved antemortem microwear. These include the maxillary right lateral incisor of M-D1-259, the maxillary left central incisor of M-D2-588, the maxillary right canine of M-S-TNN1, and the maxillary left canine of M-G4-144. High-resolution casts of these specimens were provided by Profs. Leslea Hlusko and Tim White.

Pech de l'Azé I

Site Information

Location: Pech de l'Azé I rock shelter near Carsac, France

Latitude: 44° 51' 0" N

Interior or coastal site: Interior, near the Dordogne River

Lithic Industry: Mousterian of the Acheulean tradition

Faunal Assemblage: Bovids, red deer, horse, and goat

Date: OIS 3: 50,000 to 42,000 years BP (ESR, AMS ^{14}C, and U-series dating)

Climate: Temperate woodland

Sources: Mellars, 1996; Schwartz & Tattersall, 2002; Soressi et al., 2007

Specimen information

Seven deciduous anterior teeth of the Pech de l'Aze 1 child (approximately four years old) were scanned for microwear analyses. The mandibular teeth are the right canine and lateral and central incisor, and left central incisor. The maxillary teeth are the right and left central incisors, left lateral incisor and left canine. The Rdi^1 was selected for analysis. Dental casts were provided by Prof. Jean-Jacques Hublin.

Rochelot

Site Information

Location: Cave near Saint-Angeau, France

Latitude: 45° 50' 0" N

Interior or coastal site: Interior, near the Bonnieure River

Lithic Industry: Mousterian

Faunal Assemblage: Aurochs, wild boar, fallow deer, roe deer, giant deer, steppe rhinoceros, horse, reindeer, and Neandertal. The assemblage is thought to be a hyena accumulation.

Date: end of OIS 5: 90,000 to 70,000 years BP

Climate: Temperate woodland, although the presence of reindeer and horse suggest some fluctuations to cooler, more open conditions.

Sources: Tournepiche, 1994; Tournepiche et al., 1996

Specimen information

Six permanent Neandertal teeth have been recovered from Rochelot cave, along with a few Mousterian artifacts. The small lithic assemblage, coupled with heavy carnivore damage on the faunal assemblage, has suggested that this site was a hyena den (Tournepiche et al., 1996). Some speculate the Neandertal remains were dragged into the cave by scavengers, although this remains debated (Tournepiche, 1994). The right and left mandibular canines were analyzed for microwear, and both preserved antemortem wear. The left canine was selected for analysis. Dental casts were provided by Prof. Jean-Jacques Hublin.

Saint-Césaire

Site Information

Location: La Roche à Pierrot rock shelter near Saint-Césaire, France

Latitude: 45° 45' 0" N

Interior or coastal site: Interior, near the Coran River

Lithic Industry: Châtelperronian industry

Faunal Assemblage: Steppe bison, reindeer, horse

Date: OIS 3: 36,000 years BP

Climate: Cold, open conditions

Sources: Schwartz & Tattersall, 2002; Morin, 2008

Specimen information

Teeth from one adult individual, Saint-Césaire I, were available for microwear analysis, including the mandibular right lateral and central incisors. Only the RI_2 preserved

unobscured wear. This Neandertal specimen was also subjected to stable isotope analysis, and the $^{13}\delta C$ and $^{15}\delta N$ values were -19.8 and 11.4 ‰, respectively (Bocherens et al., 2005). High-resolution casts were provided by Prof. Alejandro Pérez-Pérez.

Gibraltar

Forbes' Quarry

Site Information

Location: Quarry site near North Front, Gibraltar

Latitude: 36° 8' 0" N

Interior or coastal site: Coastal

Lithic Industry: n/a

Faunal Assemblage: n/a

Date: unknown

Climate: unknown

Sources: Schwartz & Tattersall, 2002

Specimen information

The Forbes' Quarry female Neandertal skull and dentition (GB1) was the second Neandertal fossil discovered after that of Engis. Although the exact date of the discovery is unknown, it was first reported in 1848 and recognized as a Neandertal decades later (Schwartz & Tattersall, 2002). Besides the site location, much of the stratigraphic, archaeological, and faunal assemblage context is unknown. The maxillary right lateral incisor and canine were available for study, and the incisor preserved antemortem wear. Dental casts were provided by Prof. Alejandro Pérez-Pérez.

Great Britain

Pontnewydd

Site Information

Location: Pontnewydd Cave in Denbighshire, Wales

Latitude: 53° 14' 0" N

Interior or coastal site: Interior, near the Elwy River

Lithic Industry: Mousterian of the Acheulean tradition (early Neandertal)

Faunal Assemblage: Horse, narrow-nosed rhinoceros, Merck's rhinoceros, red deer, voles, pika, wolf, bear, and spotted hyena

Date: OIS 7: 250,000 to 225,000 years BP (Uranium-Thorium and thermoluminescence)

Climate: Faunal assemblage and sedimentology studies suggests oscillations between warm, temperate conditions and more open, steppe climates.

Sources: Green et al., 1981; Green, 1984; Jenkins, D.A. 1994

Specimen information

The mandibular right lateral incisor (PN 10) was available for microwear analyses, and it did preserve antemortem wear. This specimen represents the one of the earliest dated individuals in this study, and is designated as an early Neandertal. The high-resolution cast was provided by Prof. Alejandro Pèrez-Pèrez.

Hungary

Subalyuk

Site Information

Location: Subalyuk Cave, near Cserépfalu, Hungary

Latitude: 48° 00' 0" N

Interior or coastal site: Interior, near the Tisza River

Lithic Industry: Eastern Mousterian

Faunal Assemblage: Horse, reindeer, wild goat, steppe pika, cave bear

Date: OIS 4: 70,000 to 60,000 years BP

Climate: Fauna assemblage suggests a continental steppe environment

Sources: Schwartz & Tattersall, 2002

Specimen information

The Subalyuk 1 mandible was excavated in 1932 and described in 1935. The jaw and associated postcranial remains are that of a 40 to 45-year-old female. Although the stratigraphic sequences of the cave site were not properly documented, the faunal assemblage provides an approximate date of OIS 4 (Schwartz & Tattersall, 2002).

All six mandibular anterior teeth were analyzed for dental microwear textures, and only the right canine preserved antemortem wear. The high resolution cast was provided by Prof. Peter Ungar.

Italy

Saccopastore

Site Information

Location: Gravel pit in Rome, Italy

Latitude: 41° 57' 0" N

Interior or coastal site: Interior, near the Aniene River

Lithic Industry: Pontian Mousterian

Faunal Assemblage: Horse, Merck's rhinoceros, European ass, hippopotamus, red deer, and auroch

Date: OIS 5e: 130,000 to 120,000 years BP

Climate: Temperate woodland

Sources: Schwartz & Tattersall, 2002; Giacobini & Manzi, 2005

Specimen information

The Saccopastore II Neandertal is described as an adult male, and was found in layer 3a (aka Level 7), which corresponds to OIS 5e (Schwartz & Tattersall, 2002; Giacobini & Manzi, 2005). The maxillary left and right canines were available for microwear analysis, with only the left preserving a microwear signature. High-resolution molds were taken by myself, with permission from Prof. Giorgio Manzi at the University of Rome.

Spain

Zafarraya

Site Information

Location: Zafarraya cave site near Alcaucín, Spain

Latitude: 36° 57' 05" N

Interior or coastal site: Interior, near the Madre River

Lithic Industry: Mousterian

Faunal Assemblage: Spanish ibex (90% of the bovid assemblage) horse, chamois, leopard, lynx, wild cat, hyena, dhole (*Cuon alpinus*), fox, and brown bear

Date: OIS 3: 33,500 years BP (C-14 dating)

Climate: Temperate woodland

Sources: Geraads, 1995, 1997; Hublin et al., 1995; Hublin & Trinkaus, 1998; Schwartz & Tattersall, 2002; Barroso Ruíz & de Lumley, 2006

Specimen information

Four permanent anterior teeth were available for microwear analyses. They include Z12 (LI_2), Z14 (LI^1), Z23 (RI^1), and Z24 (RI_2). The Z12 and Z24 specimens were located in unassigned layers, whereas Z14 and Z23 are associated with Layers UA and UG, respectively (Barroso Ruíz & de Lumley, 2006). All but Z14 preserved antemortem microwear signals. Dental casts were provided by Prof. Alejandro Pérez-Pérez.

Iraq

Shanidar

Site Information

Location: Shanidar cave site in the Zagros Mountains, northern Iraq

Latitude: 36° 50' 00" N

Interior or coastal site: Interior, near the Greater Zab River

Lithic Industry: Mousterian

Faunal Assemblage: Wild goat, mountain sheep, tortoise, roe deer, red deer, and wild boar

Date: OIS 4/3: 70,000 - 50,000 years BP (C-14 dating)

Climate: Mosaic between cool & dry mountainous areas and temperate, woodland hill zones

Sources: Evins, 1982; Holliday, 2000; Schwartz & Tattersall, 2003

Specimen information

Shanidar 3 was exacavated by R. Solecki in 1960, and recovered from Mousterian Layer D (Evins, 1982). The top of Layer D was C-14 dated to approximately 50,000 years BP, suggesting this individual, found lower, is older (Schwartz & Tattersall, 2003). One mandibular left canine of Shanidar 3 was available for analysis, and it preserved antemortem wear. The dental cast was provided by Prof. Erik Trinkaus.

Israel

Amud

Site Information

Location: Amud Cave, near Tiberias, Israel

Latitude: 32° 52' 00" N

Interior or coastal site: Coastal, on the northwest shore of Lake Kinneret (Sea of Galilee)

Lithic Industry: Levantine Mousterian of the Tabūn B type

Faunal Assemblage: Gazelle, fallow deer, wild goat, red deer, roe deer, aurochs, wild boar, and rhinoceros

Date: OIS 3: 55,000 to 45,000 years BP (ESR and thermoluminescence)

Climate: Mediterranean semi-arid climate (phytolith sequences)

Sources: Schwarcz & Rink, 1998; Madella & Jones, 2002; Schwartz & Tattersall, 2003; Rabinovich & Hovers, 2004

Specimen information

Dental casts of the permanent teeth from Amud 1 and 2 were available for microwear analyses. Amud 1, represented in this study by maxillary right central and lateral incisors, canine, and left central incisor, as well as the mandibular left canine, was located at the top of Level B (Schwartz & Tattersall, 2003). Amud 2, represented in this analysis by the maxillary left canine, was excavated towards the lower part of Layer B (Schwartz & Tattersall, 2003). The LC_1 of Amud 1 and LC^1 of Amud 2 preserved antemortem microwear, and dental casts were provided by Prof. Jean-Jacques Hublin and Erik Trinkaus.

Kebara

Site Information

Location: Mugharet el-Kebara cave, near Mount Carmel, Israel

Latitude: 32° 34' 00" N

Interior or coastal site: Coastal, just east of the Mediterranean Sea

Lithic Industry: Levantine Mousterian of the Tabūn B type

Faunal Assemblage: Gazelle, roe deer, wild boar, auroch, and antelope

Date: OIS 4/3: 60,000 years BP

Climate: Warm, temperate forest mixed with nearby semi-desert

Sources: Speth & Tchernov, 1998; Schwartz & Tattersall, 2003

Specimen information

All of the mandibular anterior teeth from Kebara 2 were available for microwear analyses; however, only the right canine preserved antemortem microwear. Kebara 2 is estimated to be an adult male individual who was located in a deliberate burial context in Layer 12 (Schwartz & Tattersall, 2003; Shea, 2003). Dental casts were provided by Profs. Jean-Jacques Hublin and Erik Trinkaus.

Tabūn

Site Information

Location: Mugharet et-Tabūn cave near Mount Carmel, Israel

Latitude: 32° 40' 00" N

Interior or coastal site: Coastal, just east of the Mediterranean Sea

Lithic Industry: Levantine Mousterian

Faunal Assemblage: Layer B: Horse, wild boar, roe, red, and fallow deer, gazelle, wild goat, auroch

Layer C: Hippopotamus, rhinoceros, roe deer, fallow deer, horse, wild boar, wild goat, gazelle

Date: Layer B: OIS 5: 120,000 to 100,000 years BP (ESR dating)

Layer C: OIS 6/5: 170,000 to 125,000 years BP (Thermoluminescence and ESR dating)

Climate: Colder intervals of OIS 6 would have brought semi-desert conditions, whereas the warmer periods of OIS 5 would have been dominated by warm, temperate climates

Sources: Jelinek et al., 1973; Albert et al., 1999; Schwartz & Tattersall, 2003

Specimen information

Tabūn Cave was excavated between 1929 and 1934 by D. Garrod, and the stratigraphic sequence was divided into seven levels, A through G. However, this cultural sequence was later divided into three geological units, I, II, and III (Albert et al., 1999). The Neandertal sample was located in layers B (unit I) and C (unit II) (Albert et al., 1999; Schwartz & Tattersall, 2003). Two individuals from Layer C, Tabun I (aka C1) and II, one

isolated maxillary right lateral incisor from Layer B, Series I (HPM N 7453), and two isolated teeth, maxillary left and right central incisors from Layer B, Series III (HPM N 7456) were available for microwear analyses. The LI^2 of Tabun I (C1), RI_2 of Tabun II, RI^2 from Series I, and RI^1 and LI^1 from Series III were used for analysis. Dental casts were provided by Profs. Jean-Jacques Hublin, Alejandro Pérez-Pérez, and Erik Trinkaus.

NEANDERTAL SAMPLE			
COUNTRY	**SITE**	**OIS**	**CLIMATE**
Beligum	Engis†	3	Cool
	Scladina	5e	Temperate
	Spy	3	Cool
Croatia	Krapina	6/5e	Temperate
	Vindija	3	Temperate
Czech Republic	Kůlna	3	Cool
	Ochoz	5	unknown
France	Arcy-sur-Cure	4	Cool
	Biache-Saint-Vaast	7/6	Temperate
	Combe Grenal	4	Cool
	La Chaise - Abri Suard	7/6	Temperate
	La Chaise - Abri Bourgeois-Delaunay*	6/5e	Temperate
	La Ferrassie	4	Cool
	La Quina	4/3	Cool
	Le Moustier	3	Cool
	Le Petit-Puymoyen	3	Cool
	Les Pradelles (Marillac)	3	Cool
	Monsempron	4	Cool
	Moula Guercy	5	Temperate
	Pech de l'Aze I†	3	Temperate
	Rochelot	5	Temperate
	Saint-Césaire	3	Cool
Gibaltar	Forbes' Quarry	unknown	unknown
Great Britain	Pontnewydd	7	Temperate
Hungary	Subalyuk	4	Cool
Italy	Saccopastore	5e	Temperate
Spain	Zafarraya	3	Temperate
Iraq	Shanidar	4/3	Temperate
Israel	Amud	3	Temperate
	Kebara	4/3	Temperate
	Tabūn	6/5	Temperate

Table 3.1: Summary of the Neandertal sites, OIS date, and paleoclimate reconstruction used in this study. For a more detailed description, see each individual site.

*This site is represented by both permanent and deciduous teeth. Only permanent teeth are used in the statistical analysis.
†This site is represented by only deciduous teeth, and is not included in the statistical analysis.

Figure 3.2: Map showing AMH sites used in this study.

The fossil sample: anatomically modern humans

Croatia

Vindija

Site Information

Location: Vindija cave, near Donja Voća, Croatia

Latitude: 46° 18' 0" N

Interior or coastal site: Interior, near the Drava River

Lithic Industry: Layers E and D: Late Epigravettian

Faunal Assemblage: Wild boar, wild goat, steppe bison, reindeer, moose, red deer, giant deer, wolf, fox, and arctic fox

Date: OIS 2: 22,000 to 17,500 years BP (C-14 dating)

Climate: Mosaic between somewhat temperate open and woodland conditions

Sources: Wolpoff et al., 1981; Schwartz & Tattersall, 2002; Ahern et al., 2004; Janković et al., 2006; Miracle et al., 2010

Specimen information

Two anatomically modern human specimens from the Epigravettian layers at Vindija Cave were available for analysis: 22.1, an isolated incisor, and 22.2, a maxillary right lateral incisor. Both preserved antemortem microwear, and were included in the analysis. High-resolution dental casts were provided by Prof. Alejandro Pérez-Pérez.

Czech Republic

Dolní Věstonice

Site Information

Location: Open-air sites (Dolní Věstonice I and II) on the slopes of the Pavlov Hills, Czech Republic

Latitude: 48° 53' 0" N

Interior or coastal site: Interior, near the Dyje River

Lithic Industry: Upper Paleolithic Pavlov of the Eastern Gravettian

Faunal Assemblage: Woolly mammoth, reindeer, horse, hare, wolf, and fox. Evidence of extensive hide working is found at the DV II site (West, 2001).

Date: OIS 3: 27,000 to 23,000 years BP (C-14 dating)

Climate: Fluctuations among three climate conditions: partially wooded areas of conifers and some deciduous trees, shrub and steppe, and steppe environments, depending on time and elevation.

Sources: Trinkaus & Jelínek, 1997; West, 2001; Schwartz & Tattersall, 2002; Svoboda, 2006

Specimen information

Anterior teeth from five individuals were available for microwear analysis: DV 3, 13, 14, 15, and 36. Dolní Věstonice 3 (DV 3), an adult female, was located in a flexed burial at the DV I site (Trinkaus & Jelínek, 1997). Although all maxillary and mandibular anterior teeth were available, only the RI_1 and LC_1 preserved antemortem microwear. The LC_1 was selected for analysis due to the quality of microwear features.

Dolní Věstonice individuals 13-15 are from the top and western slope of the DV II site, and were found together in a triple burial context with several grave goods, including pierced carnivore teeth and ivory pendants (Trinkaus & Jelínek, 1997; Svoboda, 2006). The DV 13 and 14 individuals represent adult males, whereas DV 15 represents an adult of unknown sex with congenital abnormalities (Trinkaus & Jelínek, 1997). All of the mandibular anterior teeth and maxillary left central incisor and left canine of DV 13 were available for microwear analysis, but only the two maxillary teeth preserved microwear. The LI^1 of DV 13 was selected for analysis. The four maxillary incisors and all mandibular anterior teeth of DV 14 were available, and the RI^2 and RI^1 and RI_2 and RI_1 preserved microwear. The RI_1 of DV 14 was selected for analysis. The four maxillary incisors, mandibular canines, and right incisors of DV 15 were available, and the RI^1 and RI_1 preserved microwear features. The RI^1 of DV 15 was selected for analysis.

A maxillary deciduous right central incisor, labeled 36/1 (aka 36a), was also available for microwear analyses; however, this individual represents an infant found on the western slope of DV II, and only postmortem scratches were recognized on the labial surface (Holliday et al., 2006; Svoboda, 2006).

High-resolution dental casts were provided by Prof. Jean-Jacques Hublin.

Pavlov I

Site Information

Location: Open-air site on the base of the Pavlov Hills, Czech Republic, 500 meters from Dolní Věstonice

Latitude: 48° 52' 0" N

Interior or coastal site: Interior, near the Dyje River

Lithic Industry: Upper Paleolithic Pavlov of the Eastern Gravettian

Faunal Assemblage: Woolly mammoth, hare, reindeer, horse, wolf, red fox, and arctic fox

Date: OIS 3: 27,000 to 25,000 years BP

Climate: Fluctuations among three climate conditions: partially wooded areas of conifers and some deciduous trees, shrub and steppe, and steppe environments, depending on time and elevation.

Sources: Schwartz & Tattersall, 2002; Svoboda, 2006; Bochenski et al., 2009

Specimen information

Ten individuals from Pavlov were available for microwear analysis; five represent adult individuals, and the other five are subadults. The adult individuals are Pavlov 1, 3, 5, 23, 25, with the first two located in the northwestern area of the site, and the last three found

in the southeastern area (Svoboda, 2006). Pavlov 1 represents a disturbed adult burial, and all the maxillary anterior teeth, with the exception of the LI^1, and the mandibular left canine and central incisor and right central and lateral incisors were available for microwear analysis. The RI^1, LI_2, and LI_1 preserved microwear features, and the RI^1 was selected for use in this study. The Pavlov 3 mandible, represented by the right canine, did not preserve microwear. The third adult individual, Pavlov 5, is represented by two isolated mandibular central incisors and both preserved antemortem microwear features. Pavlov 23 and 25, an isolated mandibular left lateral incisor and mandibular right lateral incisor, respectively, also preserved antemortem microwear.

The other five Pavlov individuals, Pavlov 13 (dc^1), 14 (dc^1), 16 (di^2), 17 (di_2), 18 (di_2), are subadults, and all preserved antemortem microwear (Hillson, 2006). High-resolution casts were provided by Prof. Jean-Jacques Hublin.

France

Aurignac

Site Information

Location: Grotte d'Aurignac, north of Aurignac, France, near the Pyrenees Mountains

Latitude: 43° 13' 0" N

Interior or coastal site: Interior, near the Rodes Brook

Lithic Industry: Upper Paleolithic: Aurignacian IV

Faunal Assemblage: Aurochs, horse, reindeer, juvenile rhinoceros, fox, cave bear, and hyena

Date: OIS 2: 12,000 years BP

Climate: Cool, open steppe conditions

Sources: Lartet, 1861; Lyell, 1863; de Sonneville-Bordes, 1959; Oakley et al., 1971; Straus, 1990

Specimen information

The cave site at Aurignac was located by a local worker in the middle of the 19th century, and the remains of 17 modern human individuals were excavated and interred in the local perish cemetery (Lyell, 1863). They were analyzed eight years later by Édouard Lartet, but the exact stratigraphic context had been forgotten by the local worker (Lyell, 1863). However, these individuals, along with mammalian fauna, were assigned to layer *a* inside the cave, and determined to be from OIS 2 (Lyell, 1863).

A series of isolated teeth, including incisors, canines, and premolars, were available for individual 4176. Two anterior teeth, an incisor and canine, preserved microwear, and the incisor was selected for analysis. High-resolution casts were provided by Prof. Jean-Jacques Hublin.

Brassempouy

Site Information

Location: Grotte du Pape near Brassempouy, France

Latitude: 43° 48' 0" N

Interior or coastal site: Interior, near the Luy de France River

Lithic Industry: Upper Paleolithic: Aurignacian

Faunal Assemblage: Horse, reindeer, wild boar, red deer, northern pike (*Esox lucius*), mollusks, badger, wolf, fox

Date: OIS 3: 35,000 to 30,000 years BP (C-14)

Climate: Cold, open steppe conditions

Sources: Dubalen, 1881; Oakley et al., 1971; Henry-Gambier et al., 2004

Specimen information

Three teeth from Brassempouy, BR 90, BR 93, and BR 94, were available for analysis. BR 93 was determined to be a permanent maxillary premolar and removed from analysis (Henry-Gambier et al., 2004). The two incisors, an isolated incisor (BR 90) and maxillary left lateral incisor (BR 94), preserved microwear. High-resolution casts were provided by Prof. Alejandro Pérez-Pérez.

Farincourt

Site Information

Location: Farincourt III cave site south of Farincourt, France

Latitude: 47° 45' 0" N

Interior or coastal site: Interior, near the Rigotte River

Lithic Industry: Upper Paleolithic: Final Magdalenian

Faunal Assemblage: Reindeer, mammoth, aurochs, bison, horse, chamois, hyena, bear, wolf, and fox

Date: OIS 2: 12,000 years BP

Climate: Cold, open steppe conditions

Sources: Joffroy & Mouton, 1946

Specimen information

One specimen from Farincourt III cave, Farincourt 1, was available for analysis. Farincourt 1 is a mandible of a young adult, and all anterior teeth were examined for

microwear textures. Only the right canine and lateral incisor preserved microwear, and the RC_1 was selected for analysis due to the quality of the microwear surface. High-resolution casts were provided by Prof. Jean-Jacques Hublin.

Isturitz

Site Information

Location: Grottes d'Isturitz near Saint-Martin-d'Arberoue, France

Latitude: 43° 20' 0" N

Interior or coastal site: Interior, near the Arberoue River (30 km from the Atlantic Ocean)

Lithic Industry: Upper Paleolithic, surrounding layers date to Solutrean

Faunal Assemblage: unknown, but surrounding layers contained horse, reindeer, and bison

Date: OIS 3/2: surrounding layers date to 40,000 to 20,000 years BP

Climate: unknown, but most likely cold, steppe conditions from surrounding faunal assemblages

Sources: Straus, 1990; Schwartz & Tattersall, 2002

Specimen information

One specimen, Ist 115 (aka Ist III 1937) was available for microwear analysis, and the mandibular right lateral incisor preserved microwear features. High-resolution casts were provided by Prof. Jean-Jacques Hublin.

Lachaud

Site Information

Location: Grotte de Saint-Sours (Grotte de Lachaud) near Terrasson-Lavilledieu, France

Latitude: 45° 07' 0" N

Interior or coastal site: Interior, near the Vézère River

Lithic Industry: Upper Paleolithic: Lower Magdalenian

Faunal Assemblage: Reindeer, horse, saiga (steppe antelope), European water vole, field vole, and common fox

Date: OIS 3: 30,000 years BP

Climate: Cool, steppe conditions

Sources: Ferembach, 1957; Cheynier, 1953, 1965

Specimen information

Two individuals from Lachaud were available for analysis. Lachaud 4 and 5, from the Proto-Magdalenian II layer, are both described as adolescents of approximately 13-14 years of age, and preserved mandibular anterior teeth (Ferembach, 1957). Lachaud 4 preserved two isolated incisors, and Lachaud 5 was represented by all mandibular anterior teeth except the lower left canine. One incisor from Lachaud 4 and the LI_1 from Lachaud 5 were selected for analysis. High-resolution casts were provided by Prof. Jean-Jacques Hublin.

Laugerie-Basse

Site Information

Location: Abri de Laugerie-Basse (Les Marseilles) near Les Eyzies-de-Tayac, France

Latitude: 44° 57' 0" N

Interior or coastal site: Interior, near the Vézère River

Lithic Industry: Upper Paleolithic: Magdalenian

Faunal Assemblage: Reindeer, aurochs, horse, trout, salmon, pike

Date: OIS 2: 15,000 to 12,000 years BP (C-14 and radiocarbon dating)

Climate: Cold, open steppe environment

Sources: Hue, 1913; de Sonneville-Bordes & Perrot, 1956; Gambier et al., 2000

Specimen information

One specimen, 14-401, was available for microwear analysis. This individual was found during the early excavations at Laugerie-Basse, and although the remains were documented and illustrated, the exact stratigraphic context of discovery is unknown (Hue, 1913). This specimen is represented by all four maxillary incisors, in which both central incisors preserved microwear, and the mandibular left lateral and central incisors and right central incisor. The mandibular left lateral and right central incisors preserved microwear; however, the LI^1 was selected for analysis due to its pristine microwear signature. High-resolution casts were provided by Prof. Jean-Jacques Hublin.

Les Rois

Site Information

Location: Les Rois rock shelter near Mouthier-sur-Boëme, France

Latitude: 45° 35' 0" N

Interior or coastal site: Interior, near the Boëme River

Lithic Industry: Upper Paleolithic: Aurignacian

Faunal Assemblage: Reindeer, horse, hyena, and fox

Date: OIS 3: 30,000 to 28,000 years BP

Climate: Cold, open steppe conditions

Sources: Vallois, 1958; Ramirez Rozzi et al., 2009

Specimen information

Six isolated incisor teeth, located within Aurignacian layer A2, were available for microwear analysis (Ramirez Rozzi et al., 2009). Five preserved microwear, including Les Rois 3, 5, 7 (LI^1, Vallois: R. 50, #45), and two unnumbered teeth. The specimen numbers represent the new labeling system, with the tooth type and original system, used by Vallois in 1958, in parentheses, where available. High-resolution casts were provided by Prof. Jean-Jacques Hublin.

Rond-du-Barry

Site Information

Location: Rond du Barry cave near Sinzelles, France

Latitude: 44° 47' 0" N

Interior or coastal site: Interior, near the Allier River

Lithic Industry: Upper Paleolithic: Magdalenian

Faunal Assemblage: Horse, ibex, reindeer, aurochs, chamois, hare, arctic fox, wolf, badger

Date: OIS 2: 17,100 years BP

Climate: Cold, open steppe conditions

Sources: de Bayle des Hermens, 1974; Pérez-Pérez et al., 2003; Grayson & Frey, 2004; Gaudzinski-Windheuser & Niven, 2009

Specimen information

One specimen from level F2 at Rond-du-Barry was available for analysis, and preserved maxillary right lateral and central incisors. Both preserved microwear features, but the RI^2 selected for analysis. High-resolution casts were provided by Prof. Alejandro Pérez-Pérez.

Saint-Germain-la-Rivière

Site Information

Location: Rock shelter near Libourne, France

Latitude: 44° 57' 0" N

Interior or coastal site: Interior, near the Dordogne River

Lithic Industry: Upper Paleolithic: Magdalenian

Faunal Assemblage: Saiga (antelope), horse, reindeer, and auroch

Date: OIS 2: 17,000 to 14,000 years BP

Climate: Cool, open steppe conditions

Sources: Gambier et al., 2000; Drucker & Henry-Gambier, 2005; Vanhaeren & d'Errico, 2005

Specimen information

Saint-Germain-la-Rivière contains two rock shelters named Grand Abri and Shelter of the Upper Terrace, which are divided by an area known as the Intermediate Talus (Vanhaeren & d'Errico, 2005). These areas have been excavated sporadically since 1929, demonstrating Magdalenian occupations. A female burial, dated to approximately 15,500 years BP, was located in the Upper Terrace in 1934, along with several isolated teeth; however, the exact stratigraphic context of the teeth are unknown (Gambier et al., 2000).

Fifteen teeth representing nine individuals were available for microwear analysis. These individuals are: 1970-7-4 (di), 1970-7-5 (canine), 1970-7-8 (dc), 1970-7-12 (LI^1), 1970-7-15 (I^1), 1970-7-16 (I^1), B3 (all permanent mandibular incisors), B4 (all permanent mandibular incisors), and B5 (Ldc_1). All nine individuals preserved antemortem microwear. High-resolution casts were provided by Prof. Jean-Jacques Hublin.

Italy

Grimaldi Caves

Site Information

Location: Grotte des Enfants (Fanciulli), Menton, Italy, near the French border

Latitude: 43° 47' 0" N

Interior or coastal site: Coastal, just north of the Mediterranean Sea

Lithic Industry: Aurignacian

Faunal Assemblage: Wild boar, red deer, roe deer, chamois, wild goat, cave bear, hyena, wolf, cave lion, marmot, and rabbit

Date: OIS 3: 30,000 to 25,000 years BP

Climate: Mosaic pattern of warm temperate woodland and mountain steppe desert

Sources: Cartailhac, 1912; Schwartz & Tattersall, 2002

Specimen information

One specimen from Grotte des Enfants, GdE 4, was available for microwear analysis. This adult male individual was radiocarbon dated to approximately 10,500 years BP; this date is controversial, however, due to the Aurignacian context of the burial. (Schwartz & Tattersall, 2002). All maxillary anterior teeth, except the LC^1, were available for microwear

texture analysis, and although all preserved antemortem microwear features, the LI^1 was selected due to the pristine condition of the microwear signature. High-resolution casts were provided by Prof. Alejandro Pérez-Pérez.

Israel

Ohalo II

Site Information

Location: Western shore of Lake Kinneret (Sea of Galilee), near Tiberias, Israel

Latitude: 32° 43' 0" N

Interior or coastal site: Coastal, near the Mediterranean Sea and Lake Kinneret

Lithic Industry: Levantine Epipaleolithic (contemporaneous with European Upper Paleolithic): Kebaran technocomplex

Faunal Assemblage: Fish, hare, tortoise, gazelle, deer, reptiles, and birds (and a rich flora and seed assemblage, including over 30 species of plants and fruits)

Date: OIS 2: 23,500 to 22,500 years BP (radiocarbon dates from charcoal)

Climate: Mosaic of lake, open forest, and grassland conditions

Sources: Nadel & Hershkovitz, 1991; Hershkovitz et al., 1995; Nadel et al., 2006

Specimen information

The Ohalo II H2 specimen, a male between the ages of 35 and 40, was discovered in 1989 after the coastal site was exposed following years of drought. This specimen's maxillary left central incisor preserved antemortem microwear features, and was used for this study. It is important to note that this specimen was found in nearly complete condition, and the maxillary right central incisor was lost before death (Hershkovitz et al., 1995).

Additionally, all the teeth, but especially the anterior dentition, demonstrated heavy attrition resembling the pattern typical of Alaskan Eskimos (Hershkovitz, 1995). High-resolution casts were provided by Prof. Erik Trinkaus.

Qafzeh

Site Information

Location: Qafzeh cave (Djebel Qafzeh) near Nazareth, Israel

Latitude: 32° 40' 0" N

Interior or coastal site: Interior, in between the Mediterranean Sea and Sea of Galilee

Lithic Industry: Layer C: Upper Paleolithic (Qafzeh 2)

Layer L (corresponds to Layer XVII): Levantine Mousterian (Qafzeh 4-7)

Layers XVII to XXIV: Levantine Mousterian (similar to Tabūn C and Skhūl B (9-11, 15)

Faunal Assemblage: Level C: Gazelle, fallow deer, red deer, roe deer, and aurochs

Levels L & XVII to XXII: Aurochs, red deer, gazelle, wild goat, fallow deer

Date: Level C: OIS 3: years BP: 30,000 years BP

Levels L & XVII to XXII: OIS 5: 120,000 to 90,000 years BP

Climate: Both layers demonstrate similar mosaic conditions of temperate woodland and mountain climates, although some suggest the abundance of gazelle in Layer C suggests a warmer and more humid climate during that time.

Sources: Bouchud, 1974; Vandermeersch, 1981; Schwarcz et al., 1988; Schwartz & Tattersall, 2003

Specimen information

Qafzeh Cave was excavated in 1933-1935 and again in 1966, 1969, 1973, and 1979 (Day, 1986; Schwartz & Tattersall, 2003). The excavators labeled the layers differently depending on one of three areas examined in the cave. While Neuville & Stekilis labeled the interior floor deposits A through M (youngest to oldest), Vandermeersch used 1-12 for the front terrace areas and I-XVIV (youngest to oldest) for the cave entrance area (called the vestibule) (Bouchud, 1974; Day, 1986; Schwartz & Tattersall, 2003). Thus, Levels C and L were excavated by Neuville & Stekilis, and Levels XVII to XXII by Vandermeersch. It was established that Neuville & Stekilis's Level L corresponded to Vandermeersch's Level XVII, making the majority of Qafzeh modern human sample contemporaneous (Bouchud, 1974). Nine individuals were available for microwear analysis, and all nine had at least one anterior tooth that preserved antemortem microwear signatures. The Qafzeh hominins included in this study and the tooth used in analysis are: Qafzeh 2 (LI^2), 4 (Rdc^1), 5 (RI^1), 6 (RI^1), 7 (LI^1), 9 (LC^1), 10 (Ldc^1), 11 (RC^1), and 15 (RC^1). Qafzeh 4 and 11 represent sub-adults, while the others are adults. High-resolution casts were provided by Profs. Jean-Jacques Hublin and Erik Trinkaus.

Skhūl

Site Information

Location: Mugharet es-Skhūl rock shelter on the southern banks of the Mount Carmel range

Latitude: 32° 37' 0" N

Interior or coastal site: Coastal, just east of the Mediterranean Sea

Lithic Industry: Levantine Mousterian

Faunal Assemblage: Wild ox, wild ass, rhinoceros, hippopotamus, gazelle, fallow deer, roe deer, red deer, boar, and hyena

Date: OIS 5: 130,000 to 100,000 years BP Although several sporadic dates exist, most seem to center around these dates. The original excavators, Garrod and Bate (1937) suggested Layer B correlated with Tabūn Layer C due to similar lithic and faunal assemblages.

Climate: Warm and humid conditions

Sources: Garrod & Bate, 1937; Day, 1986; Schwartz & Tattersall, 2003

Specimen information

Ten individuals were excavated from Skhūl Layer B during excavations in the 1930s, and three of them, Skhūl 2 (RI_1), 4 (LI^1), and 5 (RI^1), were available and preserved antemortem microwear signatures. All three individuals are estimated to be adults of approximately 30 to 40 years of age (Day, 1986). High-resolution casts were provided by Prof. Erik Trinkaus.

UPPER PALEOLITHIC HUMAN SAMPLE			
COUNTRY	**SITE**	**OIS**	**CLIMATE**
Croatia	Vindija	2	Mosaic/Temperate
Czech Republic	Dolní Věstonice	3	Mosaic/Cold
	Pavlov*	3	Mosaic/Cold
France	Aurignac	2	Cool
	Brassempouy	3	Cool
	Farincourt	2	Cool
	Isturitz	3/2	Cool
	Lachaud	3	Cool
	Laugerie-Basse	2	Cool
	Les Rois	3	Cool
	Rond-du-Barry	2	Cool
	Saint-Germain-la-Rivière*	2	Cool
Italy	Grotte des Enfants	3	Temperate
Israel	Ohalo	2	Temperate
	Qafzeh*	3	Temperate
	Shkūl	5	Temperate

Table 3.2: Summary of the anatomically modern human sites, OIS date, and paleoclimate reconstruction used in this study. For a more detailed description, see each individual site.

*This site is represented by both permanent and deciduous teeth. Only permanent teeth are used in the statistical analysis.

The modern human comparative sample. Note that data for the Aleut, Arikara, ethnic Chinese, Illinois Bluff, and Puye Pueblo samples are reported in this dissertation from Krueger and Ungar (2010).

Aleut

Site Information

Location: Aleutian Islands, Alaska, USA

Latitude: 52° 25' 0" N to 53° 54' 0" N

Interior or coastal site: Coastal, with the Bering Sea to the north and Pacific Ocean to the south

Subsistence: Raw and dried fish, sea mammals, shellfish, foxes, rodents, birds, and tubers

Non-dietary anterior tooth use: Yes

Date: Paleo-Aleut and Neo-Aleut timeframe: 3400 to 400 years BP

Climate: Oceanic and rainy, with uniform temperatures ranging from 11.1°C to -1.1°C (52°F to 30°F)

Sources: Hrdlička, 1945; Moorrees, 1957; Hoffman, 1993; Coltrain, 2010; Krueger & Ungar, 2010

Housed: National Museum of Natural History, Washington DC

Specimen Information

Ales Hrdlička collected this Aleut sample in the late 1930s from Agattu, Amaknak, Kagamil, Unmak, and Unalaska islands, all of which form part of the eastern archipelago of the Aleutian Islands (Hrdlička, 1945). These individuals have been dated by C-14, with results placing this Paleo-Aleut and Neo-Aleut sample at 3400 to 400 BP (Coltrain, 2010). The average Paleo-Aleut and Neo-Aleut $\delta^{14}C$ and $\delta^{15}N$ values were -12.3 and 19.5 and -12.7 and 20.3, respectively (Coltrain, 2010). These values suggest a similar marine diet, although the Neo-Aleuts may have relied on marine foods higher in the tropic web level (Coltrain, 2010). Twenty-four individuals preserved antemortem dental microwear signatures, and high-resolution casts were provided by Prof. Peter Ungar.

Amarna workers

Site Information

Location: Tell el-Amarna, in the province of Minya, Egypt

Latitude: 27° 39' 0" N

Interior or coastal site: Interior, on the east bank of the Nile River

Subsistence: Debated. Art suggests meat, skeletal evidence suggests malnutrition

Non-dietary anterior tooth use: No

Date: 3300 to 3280 BP, 18th Egyptian Dynasty under Pharaoh Akhenaten

Climate: Desert

Sources: Kemp, 2005; Rose, 2006

Housed: Amarna site, Egypt

Specimen Information

Although the New Kingdom Egyptian site of Amarna (Tell el-Amarna) has been excavated since 1892, the estimated 6,000 workers to have died during the approximately 20-year existence of Pharaoh Akhenaten's capital city went undiscovered until 2004 (Rose, 2006). Amarna is unique in that it was built in Middle Egypt, near the Nile River, and was abandoned shortly after Pharaoh Akhenaten's death (Rose, 2006). This provides a snapshot of New Kingdom Egyptian life for Amarna's approximately 40,000 residents. The cemetery, found near the South Tombs, has been undergoing excavation since this time. In Spring 2007, I traveled to Amarna and molded the maxillary central incisors of those individuals already excavated. Fourteen of them preserved antemortem dental microwear.

Andamanese

Site Information

Location: Port Blair, Great Andaman Island, east of India, west of Thailand

Latitude: 11° 40' 0" N

Interior or coastal site: Coastal, in between the Bay of Bengal and Andaman Sea

Subsistence: Wild pigs, fish, turtles, turtle eggs, shellfish, coconuts, wild fruit, tubers, roots, palms, nuts, honey, seeds, and grubs

Non-dietary anterior tooth use: Yes (arrow re-touching, stuff-and-cut practices)

Date: Second half of the 19th century, after the British colonized the region

Climate: Tropical, monsoon climate, with temperatures ranging from 22.5°C to 32.5°C (72.5°F to 90.5°F)

Sources: Man, 1883, 1885; Portman, 1899

Housed: Natural History Museum, London

Specimen Information

The Andamanese sample is made up of individuals from the Royal College of Surgeons, Oxford, Bonnington, and Greewell Collections found at the Natural History Museum in London, and was collected after the British colonized the Andaman Islands during the second half of the 19th century (Kruszynski, personal communication). The metadata available at the museum suggest these individuals were collected and presented to high-ranking British officials, who then returned to England and donated the remains.

Available metadata also detailed information about each burial, even as specific as the individual's name and date of death. The burial custom included decomposition on elevated, outdoor scaffolding, washing the remaining flesh from the bones, and collecting them for secondary burial. If the deceased had a surviving spouse, the skull was painted with red ochre, shells and string were tied to the zygomatic arches, and the cranium was worn by the widow or widower as a necklace. Red ochre and string attached to the zygomatic arches were found on several crania during analysis. High-resolution molds were taken by me, and 15 individuals preserved antemortem microwear signatures.

Arikara

Site Information

Location: Mobridge site (39WWI), South Dakota, USA

Latitude: 45° 32' 0" N

Interior or coastal site: Interior, on the banks of the Missouri River

Subsistence: Dried bison, peppers, grapes, pumpkins, black cherries, sunflowers, beans, squash, and corn

Non-dietary anterior tooth use: No

Date: 400 to 300 BP

Climate: Temperate, continental, grassland climate

Sources: Meyer, 1977; Tuross & Fogel, 1994; Krueger & Ungar, 2010

Housed: National Museum of Natural History, Washington DC

Specimen Information

The Arikara (aka Sahnish) sample was excavated by Stirling in the 1920s from the Mobridge site, located in north-central South Dakota (Jantz, 1973). Eighteen individuals preserved antemortem microwear signatures, and high-resolution casts were provided by Prof. Peter Ungar.

Chinese Immigrants working at the Karluk Fish Cannery

Site Information

Location: Kodiak Island, Alaska

Latitude: 57° 14' 0" N

Interior or coastal site: Coastal, on the banks of the Gulf of Alaska

Subsistence: Fish, seal, whale, sugar, flour, and rice

Non-dietary anterior tooth use: No

Date: Early 19th century

Climate: Subpolar oceanic climate, with temperatures ranging from -4°C to 16.6°C (25°F to 62°F)

Sources: Ousley et al., 2005; Krueger & Ungar, 2010; Schmidt et al., *in press*; David Hunt, personal communication

Housed: National Museum of Natural History, Washington DC

Specimen Information

This sample represents Chinese immigrants, most likely from the Guangdong Province and surrounding areas of southern China, who immigrated to Kodiak Island in search of work at the Karluk Fish Cannery on Kodiak Island (Schmidt et al., *in press*). These individuals were reportedly excavated by the fish cannery's wife and sent to Ales Hrdlička in 1931 (Ousley et al., 2005). Sixteen individuals preserved antemortem microwear signatures, and high-resolution casts were provided by Prof. Peter Ungar.

Chumash

Site Information

Location: Northern Channel Islands of California, off the coast of Santa Barbara

Latitude: 34° 1' 0" N

Interior or coastal site: Coastal, on the Pacific Ocean

Subsistence: Abalone, and many other types of fish, sea otter, Guadalupe fur seals, elephant seals, Pacific harbor seal, California sea lions, mollusks, island fox, skunk, California mule deer, birds, nuts, acorns, wild cherries, manzanita, tubers, islay, and tarweed seeds

Non-dietary anterior tooth use: No

Date: 5000 to 4000 years BP

Climate: Cool Mediterranean climate/Mediterranean dry summer subtropical climate with heavy surf, winds, and fog. Temperatures range from 10°C to 21.1°C (50°F to 70°F).

Sources: www.nps.gov; Van Valkenburgh, 1933; Walker & DeNiro, 1986; Walker & Erlandson, 1986; Kennett, 2005

Housed: Natural History Museum, London

Specimen Information

The Chumash individuals were excavated in the 1930s by Van Valkenburgh on Santa Cruz Island, part of the Santa Barbara Channel Islands. The burial site was located at "El Monton," and rock shelters were interspersed with open-air habitation sites. The excavation crew reported heavy winds and surf, and noted this was a distinguishing trait of the island that likely influenced Chumash subsistence strategy (Van Valkenburgh, 1933). Ethnographic reports suggest the Chumash relied almost entirely on fish, and stable isotope analyses of Chumash individuals from other collections support this interpretation (Van Valkenburgh, 1933; Walker & DeNiro, 1986; Walker & Erlandson, 1986). High-resolution molds were taken by me, and nineteen individuals preserved antemortem dental microwear.

Fuegian (Yahgan or Yamana)

Site Information

Location: Beagle Channel Islands, Argentine Tierra del Fuego, extreme southern South America

Latitude: 55° 43' 0" S

Interior or coastal site: Coastal, on the Pacific Ocean

Subsistence: Seals, sea lions, guanaco (*Lama guanicoe*), shellfish, fish, penguin, waterfowl

Non-dietary anterior tooth use: No

Date: Late 19th century

Climate: Oceanic climate, similar to Aleutian Islands, with temperatures ranging from -1.1°C to 11.1°C (38°F to 52°F)

Sources: Yesner et al., 2003; G. Manzi, personal communication

Housed: University of Rome, Italy

Specimen Information

The Fuegian individuals were excavated from southwestern area of Tierra del Fuego during a joint expedition between Italy and Argentina in the 1880s (Manzi, personal communication). Among other forms of cultural material, the skeletal remains returned to Italy. While one half of the skeletal collection, approximately ten individuals, resides in Rome, the other half is located in Florence. This study utilized only the collection housed in the Department of Anthropology at the University of Rome. High-resolution molds were taken by me, and high-resolution casts were also provided by Prof. David Frayer. Five of the available ten individuals preserved antemortem dental microwear.

Illinois Bluff

Site Information

Location: Jersey County, Illinois, north of St. Louis

Latitude: 39° 4' 0" N

Interior or coastal site: Interior, overlooking the Illinois River

Subsistence: Squash, marsh elder, maize, sunflowers, maygrass, smartweed, white-tailed deer, rodents, shellfish, fish, birds, berries tubers, wild fruits, and nuts.

Non-dietary anterior tooth use: Yes (tool retouching)

Date: 1400 to 1100 years BP

Climate: Humid, continental climate, temperatures range from 3°C to 25°C (37°F to 77°F)

Sources: Kelly & Cross, 1984; Mayes, 2001; Krueger & Ungar, 2010

Housed: National Museum of Natural History, Washington DC

Specimen Information

The Illinois Bluff sample was collected by P. F. Titterington in the 1920s and 1930s, and were excavated from 33 Illinois Bluff Mounds in Jersey County, Illinois (Mayes, 2001). Twenty individuals recorded antemortem microwear signatures, and high-resolution casts were provided by Prof. Peter Ungar.

Nunavut Territory

Site Information

Location: Kamarvik [LeHv-1], Silumiut[KkJg-1], and Native Point (Tunirmiut), Southampton Island [KkHh-1], northwest Hudson Bay

Latitude: Kamarvik: 64° 45' 0" N; Silumiut: 63° 41' 0" N; Native Point: 65° 00' 0" N

Interior or coastal site: All coastal sites on the Hudson Bay

Subsistence: Caribou, ringed seal, bearded seal, walrus, bowhead whale, musk oxen, eider ducks (*Somateria mollissima*)

Non-dietary anterior tooth use: Yes

Date: Kamarvik & Simumiut: Thule culture: 950 to 350 years BP

Native Point, Southampton Island: Sadlermiut: 650 to 100 years BP

Climate: Polar arctic climate, with temperatures ranging from -34°C to 5°C (-29.2°F to 41°F)

Sources: Coltrain et al., 2004; Coltrain, 2009, J. Cybulski, personal communication, Canadian Museum of Civilization archives

Housed: Canadian Museum of Civilization, Gatineau, Quebec

Specimen Information

Collins and Taylor excavated Native Point, located on the southeastern coast of Southampton Island, during the 1954-1955 field season. This site is attributed to the Sadlermiut, an Inuit population with both Thule and Dorset genetic ancestry but thought to have been isolated from other Inuit groups given unique house construction and tool tradition (Coltrain, 2009). These burials have been radiocarbon dated to 650 to 100 years BP, and have undergone stable isotope analysis (Coltrain et al., 2004; Coltrain, 2009). The average $\delta^{14}C$ and $\delta^{15}N$ values for this sample was -13.2 and 20.3, respectively, indicating they were at the top of the food web, and most likely relying predominantly on caribou, ringed seal, and seabirds (Coltrain et al., 2004; Coltrain, 2009).

The Thule burials from Kamarvik and Silumiut, located on the northwest coast of the Hudson Bay, were excavated by Charles Merbs during the 1967-1968 field season. These two sites are attributed to both the classic and modified (aka developed) Thule cultures (Coltrain et al., 2004, Coltrain, 2009). The classic Thule is distinguished by an increased reliance on whale hunting, effort in housing construction and stability, and time spent at one location during the winter months, whereas the modified Thule demonstrated a decrease in whaling and an increase in breathing-hole sealing, as well as increased mobility (Coltrain et

al., 2004). These burials have also been radiocarbon dated to 950 to 350 years BP, and their average $\delta^{14}C$ and $\delta^{15}N$ values were -14.3 and 17.5, indicating a reliance on more terrestrial mammals, such as caribou, as well as lower-level marine taxa (Coltrain, 2009).

Six individuals from Kamarvik, six from Silumiut, and 15 from Native Point preserved antemortem dental microwear, and were included in this study. High-resolution casts were produced from molds taken by me at the Canadian Museum of Civilization.

Point Hope: Ipiutak

Site Information

Location: Northwest Alaskan coast, 125 miles north of the Arctic Circle

Latitude: 68° 20' 0" N

Interior or coastal site: Coastal, on the Chukchi Sea

Subsistence: Caribou, ringed seals, and walrus (The Ipiutak remained at Point Hope only during the summer months).

Non-dietary anterior tooth use: Yes

Date: 2050 to 1450 years BP

Climate: Arctic and arid, with temperatures ranging from -31.7°C to 10°C (-25°F to 50°F)

Sources: Larsen & Rainey, 1948; Krueger, 2006; Dabbs, 2009; Brubaker et al., 2010

Housed: American Museum of Natural History, New York City

Specimen Information

The Ipiutak site is located on the Tigara (Iñupiat: Tikigaq) peninsula on the northwest coast of Alaska. It was excavated beginning in the late 1930s, and continued into the early 1940s before WWII, by Helge Larsen and Froelich Rainey. The Ipiutak culture was

identified as unique due to specialized ivory carvings unknown in previous Alaskan Eskimo or Canadian and Greenland Inuit excavations and research.

Larsen and Rainey (1948) noted the presence of 138 burials from the Ipiutak (inland Nunamiut) cemetery, distinguished from the later Tigara from the aforementioned elaborate ivory objects, multiple burials, and extended body position; however, 122 individuals are currently housed at the American Museum of Natural History and 35% of those have been deemed too fragmentary or incomplete for analysis (Dabbs, 2009). Regardless, 22 Ipiutak individuals preserved antemortem microwear features, and high-resolution molds and casts were produced by me.

Point Hope: Tigara

Site Information

Location: Northwest Alaskan coast, 125 miles north of the Arctic Circle

Latitude: 68° 20' 0" N

Interior or coastal site: Coastal, on the Chukchi Sea

Subsistence: Whales, walrus, seal, birds, fish, berries, and other edible plants (year-round occupation site

Non-dietary anterior tooth use: Yes

Date: Thule culture: 750 to 250 years BP

Climate: Arctic, with temperatures ranging from -31.7°C to 10°C (-25°F to 50°F)

Sources: Larsen & Rainey, 1948; Krueger, 2006; Dabbs, 2009; Brubaker et al., 2010

Housed: American Museum of Natural History, New York City

Specimen Information

The later Tigara site was excavated at the same time as that of the Ipiutak, and dates to 750 to 250 years BP. At this time that the Tigara Peninsula was occupied year-round, as climate change due to neoglaciation in AD 1200 (750 years BP) limited whale-hunting areas; however, Point Hope is regarded as one of the best areas for whale hunting in the world, and it is not surprising that it quickly became permanently settled (Dabbs, 2009).

Larsen and Rainey (1948) excavated 405 Tigara (coastal Taraeumiut) burials from the western edge of the peninsula, but only 349 were later identified as from the Tigara time period. These burials were characterized by very few grave goods and single, flexed burials (Larsen and Rainey, 1948). Thirty-four Tigara individuals preserved antemortem microwear signatures, and high-resolution molds and casts were produced by me.

Prince Rupert Harbour

Site Information

Location: The Boardwalk site [GbTo-31] is found on Digby Island and the Reservoir site [GbTo-33] is on adjacent Kaien Island. Both are located in Prince Rupert Harbour, northern coastal British Columbia

Latitude: 54° 17' 0" N

Interior or coastal site: Coastal, on the Pacific Ocean and near the Skeena River

Subsistence: Salmon, Pacific herring (*Clupea harrengus*), Pacific tomcod, mule deer, sea otter, seal, and dog. 92% of the faunal assemblage was fish.

Non-dietary anterior tooth use: Yes (labret use and basketry production)

Date: 4000 to 700 BP (all precontact)

Climate: Oceanic, temperate rainforest, with temperatures ranging from 1.3°C to 13.5°C (34.3°F to 56.3°F)

Sources: Cybulski, 1974, personal communication; Stewart et al., 2009; Canadian Museum of Civilization archives

Housed: Canadian Museum of Civilization, Gatineau, Quebec

Specimen Information

The Boardwalk and Reservoir sites are two of eleven sites found among the Digby and Kaien Islands in the Prince Rupert Harbour area. The area was excavated by George F. MacDonald of the Archaeological Survey of Canada during the late 1960s and early 1970s as part of the North Coast Prehistory Project (Stewart et al., 2009). The hundreds of burials excavated were determined to be of Coast Tsimshian ancestry, and displayed rich grave goods and artifacts indicative of a stratified society (Stewart et al., 2009). Moreover, trauma such as cranial vault fractures, facial and jaw fractures, and forearm fractures suggest interpersonal violence in these populations (Cybulski, 1999) Fifteen individuals from the Boardwalk site and ten from the Reservoir site preserved antemortem dental microwear signatures. High-resolution molds and casts were produced by me.

Puye Pueblo

Site Information

Location: Volcanic plateau in north-central New Mexico, part of the Jemez Mountain range

Latitude: 34° 58' 0" N

Interior or coastal site: Interior, west of the Rio Grande River

Subsistence: Maize, squash, and bean agriculture, along with yucca fruit, prickly pear, grapes, plums, beeweed, rabbits, foxes, and deer

Non-dietary anterior tooth use: No

Date: 1100 to 330 BP

Climate: Arid to semiarid desert, with temperatures ranging from 2°C to 33°C (35°F to 92°F)

Sources: Hewett, 1938; Trierweiler, 1990; Barnes, 1994; Krueger & Ungar, 2010

Housed: National Museum of Natural History, Washington DC

Specimen Information

The Puye Pueblo sample was collected by Edgar L. Hewett, in association with the Southwest Society of the Archeological Institute of America, in 1909 and excavated from Pajarito Plateau (Tewa: Tsirege), west of the Rio Grande river in New Mexico (Barnes, 1994). Eighteen individuals preserved antemortem microwear signatures, and high-resolution casts were provided by Prof. Peter Ungar.

MODERN HUMAN COMPARATIVE SAMPLES			
GROUP	**SITE/S**	**DATES (years BP)**	**CLIMATE**
Aleut	Aleutian Islands	3400-400	Oceanic and rainy
Egyptian	Amarna	3300-3280	Desert
Andamanese	Andaman Islands	19th century	Tropical, monsoon
Arikara	Mobridge, South Dakota	400-300	Temperate grassland
Chinese	Karluk cannery, Kodiak Island	19th century	Subpolar oceanic
Chumash	Northern Channel Islands	5000-4000	Cool Mediterreanean
Fuegian	Tierra del Fuego	19th century	Oceanic
Illinois Bluff	Illinois Bluff Mounds, Illinois	1400-1100	Humid, continental
Sadlermiut	Kamarvik, Simumiut, Native Point	950-100	Polar arctic
Ipiutak	Point Hope, Alaska	2050-1450	Arctic and arid
Tigara	Point Hope, Alaska	750-250	Arctic and arid
Tsimshian	Boardwalk and Reservoir, BC	4000-700	Oceanic, temperate
Puye Pueblo	Pajarito Plateau	1100-330	Desert

Table 3.3: Summary of modern human comparative samples used in this study. For more detailed information, see each specific sample.

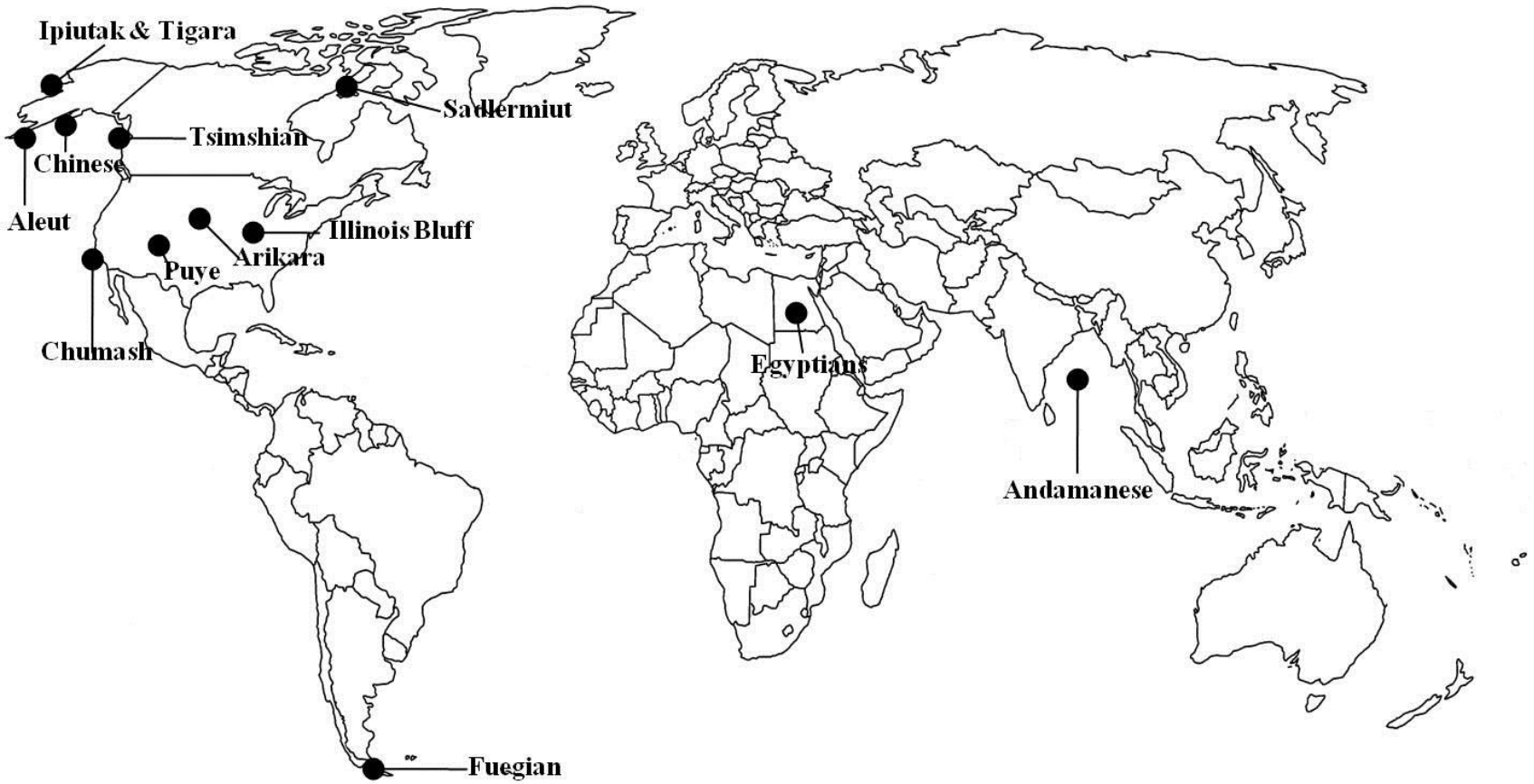


Figure 3.3: World map displaying the locations of the modern human comparative samples.

Methodology

Molding and Casting Procedure

This study utilized high-resolution replicas of fossil and modern human anterior teeth. The fossil dataset was composed of the anterior teeth (maxillary or mandibular anterior tooth, including canines, lateral incisors, and central incisors) that best preserved unobscured antemortem microwear, subject to the vagaries of fossil preservation and taphonomy. Modern human comparative datasets consist of maxillary central incisors only. However, the fossil samples consist of maxillary and mandibular central incisors, lateral incisors, and canines. The reason for the expanded range of tooth types by jaw was to utilize the largest fossil sample possible. Statistical tests, detailed below and in Chapters 5 and 6, were completed to ensure that microwear textures did not differ by tooth type or by jaw.

Some of the replicas of the fossil materials were provided by Profs. David Frayer, Jean-Jacques Hublin, Alejandro Pérez-Pérez, Peter Ungar, though I collected others myself . High-resolution casts of the Aleut, Arikara, Chinese immigrants, Illinois Bluff, and Puye Pueblo were provided by Prof. Peter Ungar. Casts of some of the Fuegian material was provided by Prof. David Frayer. I collected remaining modern human comparative samples, including the Amarna workers, Andamanese, Chumash, Nunavut Territory, Point Hope Ipiutak, Point Hope Tigara, and Prince Rupert Harbour.

All molds were prepared in the same manner. First, the labial surface of the anterior tooth or teeth were gently cleaned with acetone and cotton swabs. Second, President's Jet (regular body polysiloxane, Coltène-Whaledent) was used as the medium for mold production. Two sets of molds were taken: the first was to ensure the remaining

dust or soil was removed from the tooth surface, and the second set was for production of high-resolution casts. The casts were produced at the University of Arkansas using Epotek 301 two-part base and hardener (Epoxy Technologies). Each tooth was then examined for dental microwear features using a white-light confocal profiler located at the University of Arkansas.

Dental Microwear Texture Analysis

Following the protocols set forth by Scott et al., 2005 and 2006 and Krueger & Ungar, 2010, the labial surface, just above the incisal edge, of each anterior tooth was examined for dental microwear features. All specimens were examined using a Sensofar Plμ white-light confocal profiler (Solarius Development Inc., Sunnyvale, California), which has a lateral sampling of 0.18 μm and a vertical resolution of 0.005 μm (Scott et al., 2006). Using a 100x objective lens with a field of view of 138 x 102 μm, four adjacent scans of each enamel surface were taken, creating a three-dimensional point cloud totaling 276 x 204 μm (Scott et al., 2006). The four scans representing each tooth were then leveled and examined for defects, such as soil, preservative, or dust, using Solarmap Universal software (Solarius Development Inc., Sunnyvale, California). Any defects found were removed prior to analysis. The scans were then uploaded into Toothfrax and SFrax scale-sensitive fractal analysis software packages (Surfract, www.surfract.com) for analysis.

Scale-sensitive fractal analysis operates on the principle that the apparent area of a surface, length of a profile, or volume of an object changes with the scale of observation (Scott et al., 2005, 2006). For example, the pavement of a road may seem smooth to the

driver of a car (coarse scale), but becomes rough and uneven to an ant attempting to cross it (fine scale). Thus, the surface changes with the scale of observation. Using this principle, five variables, complexity, scale of maximum complexity, anisotropy, textural fill volume, and heterogeneity, are used to characterize microwear features based not on the tradition pits and scratches, but on textures.

Complexity or Area-scale fractal complexity (*Asfc*), is a measure of the change of surface roughness over the scale of observation (Scott et al., 2005, 2006). The area-scale tiling algorithm is used to calculate this variable, in which differently sized triangles, larger at coarse scales, and progressively smaller at finer scales, are laid down on the surface. The areas of these triangles, at any particular scale, are summed and divided by the planometric (two-dimensional) area of that surface in order to calculate the relative area ($RelA_{scale}$) (Scott et al., 2006). The log-log plot of relative area over the range of scales (7200 μm^2 to 0.02 μm^2) is then multiplied by -1000, and the slope of the steepest part of the curve fit to the log-log plot is the Area-scale fractal complexity value (Scott et al., 2006). Past research has shown that microwear features of varying sizes and shapes will produce a high *Asfc* value (Scott et al., 2005, 2006).

While the *Asfc* variable is calculated from the slope of the steepest part of the curve, the steepest part of the curve itself can be helpful when characterizing dental microwear textures. This describes the Scale of Maximum Complexity (*Smc*), or the finest scale at which the microwear surface is most complex (Scott et al., 2006). Microwear textures with large features at a coarse scale will have high *Smc* values.

Anisotropy or exact proportion Length-scale anisotropy of relief (*epLsar*) is a measure of surface orientation (Scott et al., 2005, 2006). A length-scale rotational

algorithm is used to determine this variable, in which line segments of different lengths, fewer, longer segment lengths at coarser scales, and progressively more, shorter segment lengths at finer scales, (shorter lengths provide a more exact fit) are laid down on a surface profile (depth profile) (Scott et al., 2005, 2006). The lengths of these line segments, at a given scale (I used 1.8 microns), are summed and divided by the estimated length of the profile in order to calculate the relative length ($RelL_{scale}$) (Scott et al., 2006). The relative length differs depending on the orientation if the surface roughness displays directionality. Thus, relative lengths at different orientations (thirty-six 5° intervals, or 180°), now defined as vectors, are calculated and normalized using the exact proportion method (Scott et al., 2006). These 36 normalized relative length vectors can be plotted in a rosette diagram, and the length of the mean vector is the *epLsar* value (Scott et al., 2006). A surface with many parallel scratches demonstrates high anisotropy values.

Textural fill volume (*Tfv*) is a measure of surface volume, and the volume-filling versus scale square cuboid filling algorithm is used to calculate this variable (Scott et al., 2006). Cuboids of varying sizes are used to fill surface relief; that is, larger cuboids are used at coarse scales, and progressively smaller cuboids are used at finer scales (Scott et al., 2006). However, these cuboids not only differ in overall size, but can differ in dimension (think square v. rectangle). The difference in size and dimension of the cuboid is determined by the scale of observation and the surface being filled, respectively. Namely, the algorithm begins at the largest coarse-scale cuboid size that can fit the dimensions of the surface without being higher than the highest point on that surface (Scott et al., 2006). As the overall size of the cuboid reduces at finer scales, more and more cuboids are needed to fill the surface, increasing the overall volume being filled

(Scott et al., 2006). The fill volume at the coarse scale (10 µm in this study) is called the structural fill volume, and only describes the overall shape of the surface (i.e. concave molar facet or convex labial incisor surface). The fill volume at the fine scale (2 µm in this study) is defined as the textural fill volume, and this describes the volume of the microwear features. The textural fill volume is calculated by subtracting the structural fill volume from the total volume filled (Scott et al., 2006). A surface with large, deep pits would demonstrate high *Tfv* values.

Lastly, the Heterogeneity of Area-scale fractal complexity (*HAsfc*) is a measure of variation in surface textures across a scan (Scott et al., 2006). Each scan is divided into equal numbers of rows and columns at difference scales. For example, the coarse scale begins at 2x2, meaning two equally sized rows and columns, and gets progressively finer until each scan is divided into 11 rows by 11 columns. Two forms of the *HAsfc* variable, 3x3 and 9x9, labeled $HAsfc_9$ and $HAsfc_{81}$, respectively, have been used most frequently in past microwear texture analyses.

Statistical Analyses

Statistical analyses are partitioned into four general linear models. The first model compares anterior dental microwear signatures within each fossil hominin sample. A two-factor multivariate analysis of variance (MANOVA) is performed on rank transformed data (Conover & Iman, 1981), with tooth type (central incisor, lateral incisor, and canine) and jaw (mandible and maxilla) as the factors and each texture attribute as dependent variables. Significant variation is not found in either the Neandertal or anatomically modern human model, so further statistical tests are unnecessary.

The second entailes comparisons of data for the modern human baseline series. A multivariate analysis of variance (MANOVA) is conducted on rank transformed data (Conover & Iman, 1981), with the samples as independent variables, and each texture attribute as dependent variables. Since significant variation is found in the overall model, analyses of variance (ANOVAs) for individual texture attributes and pairwise comparisons tests for the groups are applied to determine the sources of significant variation as necessary. Both Tukey's *post hoc* HSD and Fisher's *a priori* LSD tests are used to balance risks of Type I and Type II errors (Cook & Farewell, 1996). It should be noted that Tukey's HSD test results are used as the benchmark for significance, though Fisher's LSD test results are considered suggestive, with $p < 0.05$ for this test but not the HSD test, implying marginal significance.

The third linear model is divided into a two-factor and one-factor MANOVA for the Neandertal sample. The two-factor MANOVA is performed on ranked data for the Neandertal sample, with location and climate type as the factors. Locations are divided into northern, central, and southern subgroups by latitude, and the climate types are warm-woodland and cold-open-steppe. In order to maximize the available sample size for location and climate, the time interval factor is tested separately, and a one-factor MANOVA is performed on ranked data for the Neandertal sample. Time intervals are divided by OIS number, and are represented by OIS 6/5, 5, 4, and 3.

These divisions reflect a compromise between available sample sizes from each combination of factors. This allows for the maximum power of the test given small samples, yet still identifies effects of location, climate and time on microwear textures in the Neandertal sample. Single classification MANOVAs, ANOVAs for individual

texture attributes, and pairwise comparisons tests for the groups are used to determine the sources of significant variation as necessary. Both Tukey's *post hoc* HSD and Fisher's *a priori* LSD tests are used to balance risks of Type I and Type II errors (Cook & Farewell, 1996).

The final linear model is again a two-factor and one-factor MANOVA for the anatomically modern human sample. The two-factor MANOVA is performed on ranked data for the anatomically modern human sample, with location and climate type as the factors. Locations and climate types are divided the same way as the Neandertal sample. The one-factor MANOVA is performed on ranked data for the AMH sample, with time interval again as the factor; however, the time intervals are restricted to OIS 3 and 2. As with the Neandertal sample, ANOVAs for individual texture attributes and pairwise comparisons tests are used to determine the sources of significance, if needed. Again, both Tukey's *post hoc* HSD and Fisher's *a priori* LSD tests are used to balance risks of Type I and Type II errors (Cook & Farewell, 1996).

CHAPTER FOUR: MODERN HUMAN COMPARATIVE SAMPLES

Results

The modern human comparative samples vary significantly in all five dental microwear texture attributes. The overall MANOVA model indicates significant differences in incisor microwear textures between the groups, and the individual ANOVAs pinpoint those differences to be in complexity, scale of maximum complexity, anisotropy, textural fill volume, and both variants of heterogeneity. The analytical and descriptive statistics are presented in Tables 4.1 and 4.2, two-dimensional and three-dimensional photosimulations of each group are found in Figure 4.1, and charts of each texture attribute by group are illustrated in Figures 4.2-4.7. Results and pairwise comparisons tables (Tables 4.3 to 4.8) for each texture attribute will be presented and discussed separately, and interpretations will follow.

MANOVA				
	Test statistic	***F***	**df**	***p***
Pillai's Trace	1.226	5.22	72, 1464.00	0.00
Wilks' λ	0.213	5.96	72, 1306.11	0.00
Holtelling's Trace	2.038	6.72	72, 1424.00	0.00
ANOVAs				
	Sum of Squares	***F***	**df**	***p***
Asfc	643769.49	16.99	12	0.00
Smc	310932.79	5.90	12	0.00
epLsar	314432.50	5.82	12	0.00
Tfv	556121.63	13.20	12	0.00
$HAsfc_{9}$	251325.71	4.40	12	0.00
$HAsfc_{81}$	436201.20	9.07	12	0.00

Table 4.1: Analytical statistics.

Group		***Asfc***	***Smc***	***epLsar***	***Tfv***	***HAsfc*** $_{9}$	***HAsfc*** $_{81}$
Aleut (*n* =24)	Mean	0.93	0.40	0.0030	7434.50	0.38	0.61
	Median	0.90	0.27	0.0030	7334.67	0.38	0.55
	SD	0.45	0.36	0.0011	5272.19	0.07	0.12
Amarna (*n* =14)	Mean	0.45	1.01	0.0034	2496.82	0.38	0.59
	Median	0.45	0.82	0.0032	1155.68	0.38	0.61
	SD	0.01	1.04	0.0012	3071.31	0.09	0.08
Andamanese (*n* =24)	Mean	0.91	0.65	0.0031	1559.29	0.41	0.59
	Median	0.74	0.51	0.0025	1127.43	0.40	0.57
	SD	0.59	0.45	0.0015	1965.24	0.12	0.18
Arikara (*n* =18)	Mean	0.77	0.38	0.0036	1897.76	0.37	0.56
	Median	0.65	0.27	0.0032	634.31	0.36	0.55
	SD	0.40	0.22	0.0016	2466.36	0.08	0.12
Chinese immigrants (*n* =16)	Mean	0.67	0.35	0.0038	4011.93	0.44	0.66
	Median	0.61	0.27	0.0034	2200.81	0.45	0.61
	SD	0.27	0.15	0.0016	4924.00	0.08	0.17
Chumash (*n* =19)	Mean	0.92	0.70	0.0035	6532.50	0.44	0.64
	Median	0.79	0.42	0.0035	3465.40	0.42	0.61
	SD	0.44	0.57	0.0014	6429.48	0.12	0.18
Fuegian (*n* =5)	Mean	0.71	13.14	0.0034	9151.36	0.47	0.68
	Median	0.70	3.86	0.0035	9174.32	0.49	0.66
	SD	0.24	23.11	0.0003	4064.72	0.14	0.08
Illinois Bluff (*n* =20)	Mean	0.97	0.32	0.0027	1950.52	0.40	0.57
	Median	0.87	0.34	0.0025	594.39	0.36	0.55
	SD	0.37	0.13	0.0013	2989.45	0.08	0.09
Nunavut Territory (*n* =27)	Mean	3.28	1.11	0.0020	12449.27	0.60	1.09
Sadlermiut	Median	2.60	0.42	0.0018	12905.65	0.47	1.05
	SD	2.13	1.81	0.0010	3464.04	0.32	0.38
Ipiutak (*n* =22)	Mean	3.43	0.34	0.0020	12143.02	0.66	1.36
	Median	2.27	0.21	0.0018	12842.59	0.60	1.26
	SD	3.03	0.28	0.0008	4253.49	0.31	0.80
Tigara (*n* =34)	Mean	1.20	0.35	0.0032	7296.02	0.53	0.89
	Median	0.82	0.34	0.0029	6269.71	0.48	0.72
	SD	0.99	0.12	0.0015	5391.20	0.26	0.46
Prince Rupert Harbour (*n* =25)	Mean	1.85	0.43	0.0024	5766.64	0.46	0.70
Tsimshian	Median	1.81	0.34	0.0019	3079.71	0.46	0.68
	SD	0.78	0.25	0.0013	5196.40	0.12	0.20
Puye Pueblo (*n* =18)	Mean	1.24	0.31	0.0040	5093.03	0.48	0.75
	Median	0.87	0.27	0.0039	4284.68	0.45	0.63
	SD	1.01	0.22	0.0012	4183.08	0.14	0.32

Table 4.2: Descriptive statistics.

A
2.8
µm
E
1.2
µm
B
1.9
µm
F
1.8
µm
C
1.7
µm
G
3.3
µm
D
2.5
µm
H
2.0
µm

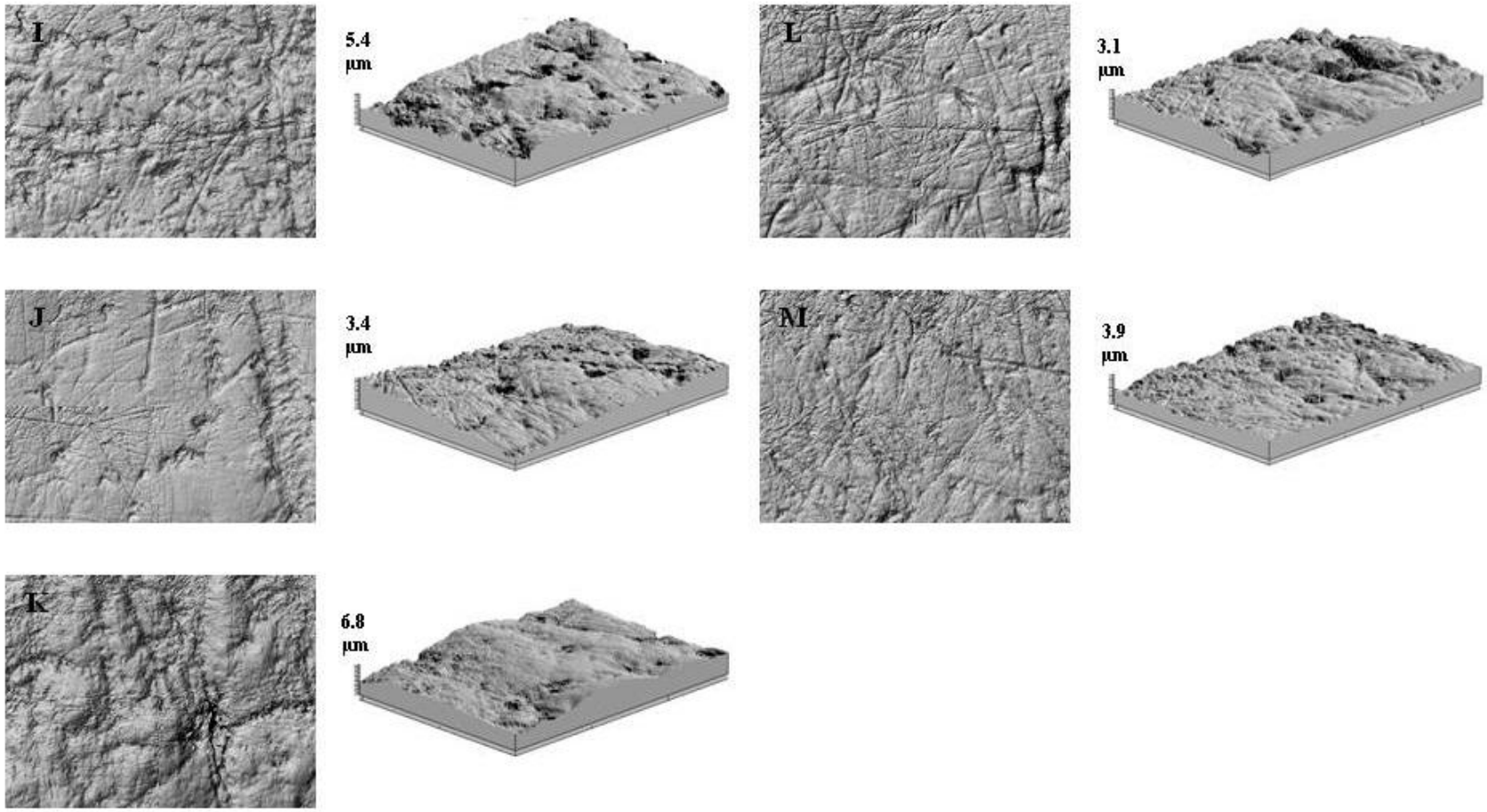


Figure 4.1: Two- and three-dimensional point cloud examples of each modern human comparative sample. A=Aleut, NMNH 378302; B=Amarna, S23; C=Andamanese, NHML 2094; D= Arikara, NMNH 325384; E=Chinese immigrant, NMNH 364435; F=Chumash, NHML 1388; G= Fuegian, UoR 6; H= Illinois Bluff, NMNH 379785; I=Nunavut Territory, CMoC XIV-C-343; J=Ipiutak, AMNH 179; K=Tigara, AMNH 265; L=Prince Rupert Harbour, CMoC XIV-B-347; M=Puye, NMNH 262069.

Complexity (Asfc)

MATRICES OF PAIRWISE DIFFERENCES: COMPLEXITY (*Asfc*)												
	Al	Am	And	Ar	CI	Ch	Fu	IL	NT	Ip	Ti	PRH
Am	**-74.56**											
And	-10.14	64.42*										
Ar	-22.19	52.37*	-12.05									
CI	-35.08	39.47	-24.95	-12.90								
Ch	-1.64	**72.92**	8.50	20.55	33.44							
Fu	-25.47	49.09	-15.33	-3.28	9.61	-23.83						
IL	11.13	**85.69**	21.27	33.32	46.21*	12.77	36.60					
NT	**105.67**	**180.23**	**115.81**	**127.86**	**140.76**	**107.31**	**131.14**	**94.54**				
Ip	**90.27**	**164.83**	**100.41**	**112.46**	**79.15**	**91.91**	**115.75**	**79.15**	-15.40			
Ti	11.94	**86.49**	22.07	34.12*	47.02*	13.57	37.41	0.81	**-93.74**	**-78.34**		
PRH	**77.99**	**152.55**	**88.13**	**100.18**	**113.07**	**79.63**	**103.46**	**66.86**	-27.68	-12.29	**66.05**	
Pu	12.51	**87.06**	22.64	34.69	47.59*	14.15	37.98	1.38	**-93.17**	**-77.77**	0.57	**-65.48**

Table 4.3: Pairwise comparisons for complexity (*Asfc*).

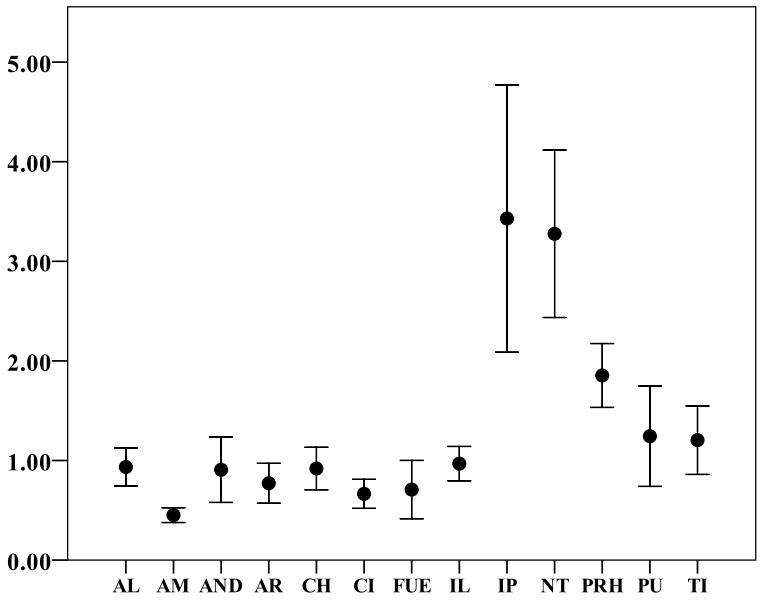


Figure 4.2: Box-and-whisker plots of complexity (*Asfc*) by sample.

Al=Aleut; Am=Amarna; And=Andamanese; Ar=Arikara; CI=Chinese immigrants; Ch=Chumash; Fu=Fuegian; IL=Illinois Bluff; NT=Nunavut Territory Sadlermiut; Ip=Ipiutak; Ti=Tigara; PRH=Prince Rupert Harbour Tsimshian; Pu=Puye Pueblo.

Tukey's HSD pairwise comparisons tests indicate that the Amarna sample has significantly lower *Asfc* values than eight samples, including the Aleut, Illinois Bluff, Puye, Ipiutak, Tigara, Chumash, Nunavut Territory, and Prince Rupert Harbour samples. Fisher's LSD results reveal additional marginal differences, with Amarna having marginally lower complexity values than the Arikara and Andamanese samples. These results indicate that the complexity values of the Amarna sample differ according to Tukey's and/or Fisher's test results from all other modern human comparative samples with the exception of the Chinese immigrants and Fuegian groups. Indeed, the Amarna sample's mean *Asfc* is the lowest of all other groups with a value of 0.45.

Tukey's HSD comparisons also show that the Ipiutak, Nunavut Territory, and Prince Rupert Harbour samples exhibit significantly higher complexity values than all other modern human samples except each other. That is, the Ipiutak sample is significantly different from all other samples except the Nunavut Territory and Prince Rupert Harbour groups, the Nunavut Territory sample is significantly different from all other samples but the Ipiutak and Prince Rupert Harbour groups, and the Prince Rupert Harbour sample differ from all but the Ipiutak and Nunavut Territory groups. Fisher's LSD comparisons did not add any marginally significant results, indicating these three groups vary from the others by a considerable margin. Indeed, the mean *Asfc* values for the Ipiutak, Nunavut Territory, and Prince Rupert Harbour sample are 3.43, 3.28, and 1.85, respectively.

It is especially interesting that these three arctic samples differ from the other two arctic samples in this study. Moreover, the two groups that lived at Point Hope, the Ipiutak and Tigara, differ significantly in complexity from each other. Lastly, the

Fisher's LSD comparisons indicate a small number of marginal differences. The Tigara, Illinois Bluff, and Puye samples are marginally higher in *Asfc* than the Chinese immigrant group, and the Tigara sample is also marginally higher than the Arikara.

MATRICES OF PAIRWISE DIFFERENCES: SCALE OF MAXIMUM COMPLEXITY (*Smc*)												
	Al	Am	And	Ar	CI	Ch	Fu	IL	NT	Ip	Ti	PRH
Am	**87.75**											
And	72.10*	-15.64										
Ar	13.30	-74.45*	-58.81*									
CI	8.32	-79.42*	-63.78*	-4.98								
Ch	**70.37**	-17.38	-1.74	57.07*	62.04*							
Fu	**123.80**	36.06	51.70	110.51*	**115.48**	53.44						
IL	3.20	**-84.54**	-68.90*	-10.09	-5.12	-67.16*	**-120.60**					
NT	45.40*	-42.35	-26.70	32.10	37.08	-24.97	-78.40*	-42.20*				
Ip	-21.90	**-109.64**	**-94.00**	-35.19	-30.22	**-92.26**	**-145.70**	-25.10	**-67.30**			
Ti	18.81	-68.94*	-53.29*	5.51	10.49	-51.56*	-104.99*	15.61	-26.59	40.71*		
PRH	31.12	-56.62*	-40.98	17.83	22.80	-39.24	-92.68*	27.92	-14.28	53.02*	12.31	
Pu	-22.92	**-110.67**	**-95.03**	-36.22	-31.25	**-93.29**	**-146.73**	-26.13	**-68.32**	-1.03	-41.73*	-54.05*

Table 4.4: Pairwise comparisons for scale of maximum complexity (*Smc*).

Scale of maximum complexity (Smc)

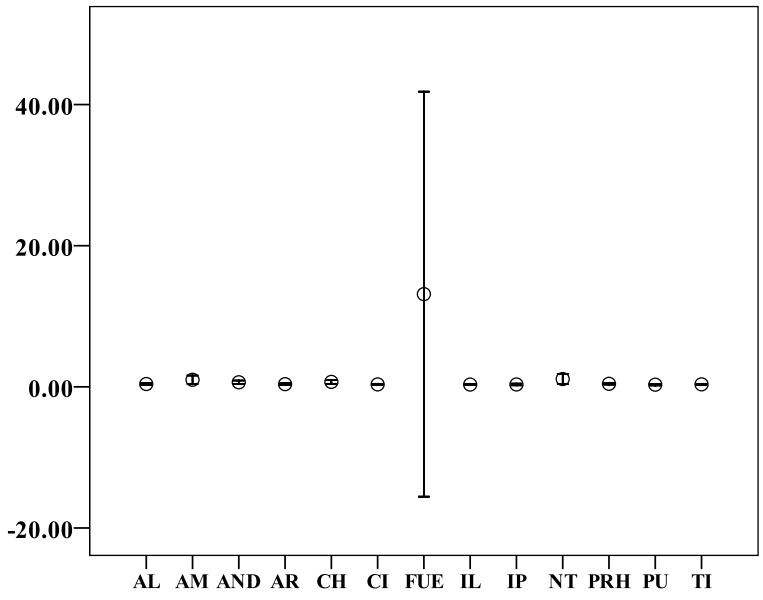


Figure 4.3a: Box-and-whisker plots of *Smc* by sample.

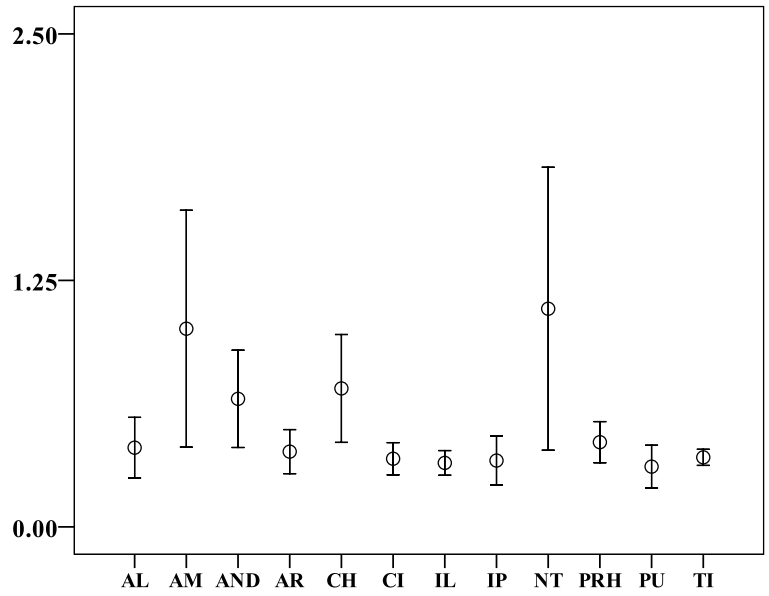


Figure 4.3b: Box-and-whisker plots of scale of maximum complexity (*Smc*) by sample without the Fuegians.

Al=Aleut; Am=Amarna; And=Andamanese; Ar=Arikara; CI=Chinese immigrants; Ch=Chumash; Fu=Fuegian; IL=Illinois Bluff; NT=Nunavut Territory Sadlermiut; Ip=Ipiutak; Ti=Tigara; PRH=Prince Rupert Harbour Tsimshian; Pu=Puye Pueblo.

Tukey's HSD pairwise comparisons tests indicate that the Fuegian sample has significantly higher *Smc* values than the Aleut, Chinese immigrants, Illinois Bluff, Puye, and Ipiutak and LSD tests show marginally higher values than the Arikara, Tigara, Nunavut Territory, and Prince Rupert Harbour samples. Moreover, the Amarna sample has significantly higher values than the Aleut, Illinois Bluff, Puye, and Ipiutak, and marginally higher values than the Arikara, Chinese immigrants, Tigara, and Prince Rupert Harbour samples.

The Chumash, Andamanese, and Nunavut Territory samples have significantly higher *Smc* values than the Ipiutak and Puye, with the Chumash also demonstrating significantly higher values than the Aleut. The Prince Rupert Harbour sample has a marginally higher *Smc* than the Puye and Ipiutak. The Chumash and Andamanese *Smc*

values are marginally higher than those of the Arikara, Chinese immigrants, Illinois Bluff, and Tigara samples, while the Andamanese also has marginally higher values than those of the Aleut. Lastly, the Nunavut Territory group is marginally higher than the Aleut and Illinois Bluff, and the Tigara is marginally higher than the Ipiutak sample.

Anisotropy (epLsar)

Tukey's HSD pairwise comparisons show that the Ipiutak and Nunavut Territory samples have significantly lower *epLsar* values than six groups, including the Arikara, Chinese immigrants, Puye, Amarna, Tigara, and Chumash samples. Moreover, Fisher's LSD pairwise comparisons indicate the Ipiutak and Nunavut Territory samples have marginally lower anisotropy values than the Aleut, Illinois Bluff, Andamanese, and Fuegian groups. The Ipiutak and Nunavut Territory samples do not differ from one another or the Prince

MATRICES OF PAIRWISE DIFFERENCES: ANISOTROPY (*epLsar*)												
	Al	Am	And	Ar	CI	Ch	Fu	IL	NT	Ip	Ti	PRH
Am	23.47											
And	-2.05	-25.52										
Ar	28.33	4.85	30.37									
CI	34.13	10.65	36.17	5.80								
Ch	25.42	1.95	27.47	-2.90	-8.70							
Fu	34.59	11.11	36.63	6.26	0.46	9.16						
IL	-16.59	-40.06	-14.54	-44.91*	-50.71*	-42.01	-51.18					
NT	-56.71*	**-80.19**	-54.67*	**-85.05**	**-90.84**	**-82.14**	-91.31*	-40.13*				
Ip	-57.72*	**-81.19**	-55.68*	**-86.05**	**-91.85**	**-83.16**	-92.31*	-41.13*	-1.00			
Ti	9.01	-14.46	11.06	-19.32	-25.11	-16.41	-25.58	25.60	**65.73**	**66.73**		
PRH	-39.55*	-63.03*	**-37.51**	-67.88*	**-77.68**	**-64.98**	-74.14*	-22.97	17.17	18.17	-48.56*	
Pu	53.02*	29.55	55.07*	24.69	18.90	27.60	18.43	69.61*	**109.74**	**110.74**	44.01*	**92.57**

Table 4.5: Pairwise comparisons for anisotropy (*epLsar*).

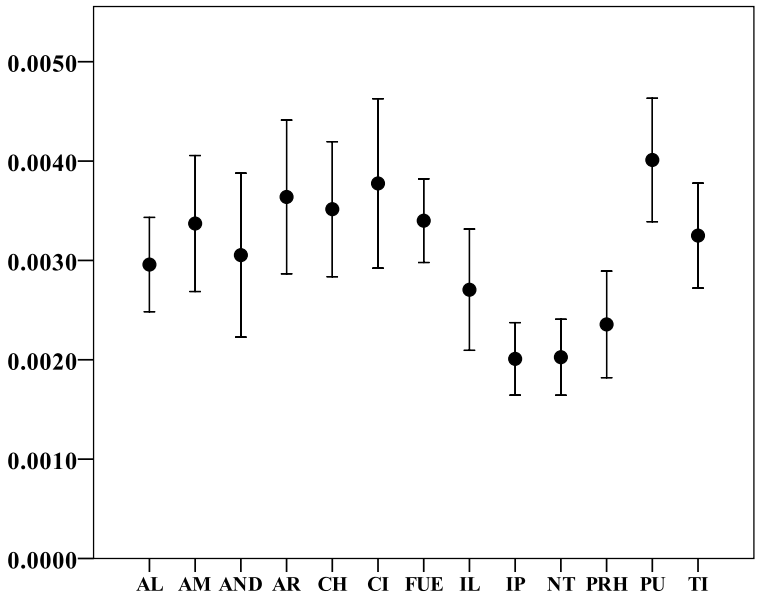


Figure 4.4: Box-and-whisker plots of anisotropy (*epLsar*) by sample.

Al=Aleut; Am=Amarna; And=Andamanese; Ar=Arikara; CI=Chinese immigrants; Ch=Chumash; Fu=Fuegian; IL=Illinois Bluff; NT=Nunavut Territory Sadlermiut; Ip=Ipiutak; Ti=Tigara; PRH=Prince Rupert Harbour Tsimshian; Pu=Puye Pueblo.

Rupert Harbour sample. The Prince Rupert Harbour sample has significantly lower *epLsar* values than the Chinese immigrants, Puye, and Chumash, and marginally lower ones than the Aleut, Arikara, Amarna, Tigara, and Fuegian groups. These results are not surprising considering the Ipiutak, Nunavut Territory, and Prince Rupert Harbour samples have the lowest anisotropy means, with values of 0.0020, 0.0020, and 0.0024, respectively.

Interestingly, the Ipiutak, Nunavut Territory, and Prince Rupert Harbour samples differ significantly (Tukey's test) or marginally (Fisher's test) from the other two arctic samples. This is a similar outcome as the complexity attribute. Also similar to the complexity result is the significant difference in anisotropy between the two Point Hope samples.

There are additional marginal differences between groups in anisotropy. The Aleut, Illinois Bluff, Tigara, and Andamanese values are marginally lower than that of the Puye sample, and the Illinois Bluff values are also marginally lower than the Arikara and Chinese immigrant samples.

Textural fill volume (Tfv)

MATRICES OF PAIRWISE DIFFERENCES: TEXTURAL FILL VOLUME (*Tfv*)												
	Al	Am	And	Ar	CI	Ch	Fu	IL	NT	Ip	Ti	PRH
Am	**-67.28**											
And	**-77.48**	-10.20										
Ar	**-70.87**	-3.59	6.61									
CI	-45.56*	21.71	31.92	25.31								
Ch	-15.31	51.96*	62.17*	55.56*	30.25							
Fu	26.79	93.76*	**103.97**	97.36*	72.05*	41.80						
IL	**-79.39**	-12.11	-1.91	-8.52	-33.83	**-64.08**	**-105.88**					
NT	**61.80**	**129.08**	**139.28**	**132.67**	**107.36**	**77.11**	35.31	**141.19**				
Ip	**59.96**	**127.24**	**137.44**	**130.83**	**105.52**	**75.27**	33.47	**139.35**	-1.84			
Ti	-0.15	**67.13**	**77.33**	**70.72**	45.41*	15.16	-26.64	**79.24**	**-61.95**	**-60.11**		
PRH	-16.11	51.16*	**61.37**	54.76*	29.45	-0.80	-42.60	**63.28**	**-77.91**	**-76.07**	-15.96	
Pu	-22.40	44.88*	55.08*	48.47*	23.17	-7.08	-48.88	56.99*	**-84.19**	**-82.36**	-22.25	-6.28

Table 4.6: Pairwise comparisons for textural fill volume (*Tfv*).

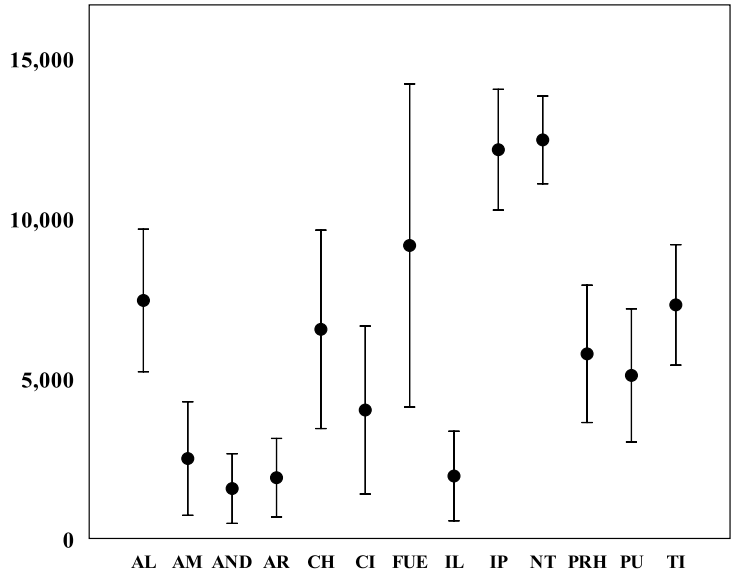


Figure 4.5: Box-and-whisker plots of textural fill volume (*Tfv*) by sample.

Tukey's HSD pairwise comparisons indicate that the Ipiutak and Nunavut Territory samples are both significantly higher in *Tfv* than all other samples, with the exception of each other and the Fuegians. That is, these two high arctic samples demonstrate higher textural fill volume than the Aleut, Arikara, Chinese immigrants, Illinois Bluff, Puye, Amarna, Tigara, Andamanese, Chumash, and Prince Rupert Harbour. This is not surprising considering these two samples possess the two highest *Tfv* means than any other group, with the Ipiutak and Nunavut Territory values calculated at 12143 and 12449, respectively.

The Aleut and Tigara samples are both significantly higher in fill volume than the Arikara, Illinois Bluff, Amarna, and Andamanese samples, and both are also marginally higher than the Chinese immigrants. These two samples have similar *Tfv* means, with the Aleut value being 7434 and the Tigara value being 7296. The remaining arctic sample, the Prince Rupert Harbour group, is significantly higher in fill volume than the Illinois Bluff and Andamanese and marginally higher than the Arikara and Amarna samples. The Puye results are somewhat similar to those of the Prince Rupert Harbour sample, although the former demonstrates only marginally higher *Tfv* values than the, Illinois Bluff, Andamanese, Arikara, and Amarna samples.

The Fuegian sample also demonstrates significant and marginal differences within the Tukey's and Fisher's tests, respectively. These tests indicate that the Fuegians are significantly higher in fill volume than the Illinois Bluff and Andamanese samples, and marginally higher than the Arikara, Chinese immigrants, and Amarna individuals. Lastly, the Chumash sample has significantly higher fill volume values than the Illinois Bluff and marginally higher values than the Arikara, Amarna, and Andamanese samples.

Heterogeneity 3x3 ($HAsfc_9$)

MATRICES OF PAIRWISE DIFFERENCES: HETEROGENEITY 3X3 (*HAsfc* $_9$)												
	Al	Am	And	Ar	CI	Ch	Fu	IL	NT	Ip	Ti	PRH
Am	-1.15											
And	10.77	11.92										
Ar	-14.36	-13.21	-25.13									
CI	38.04	39.2	27.28	52.40*								
Ch	26.96	28.11	16.19	41.32	-11.09							
Fu	50.07	51.22	39.30	64.43	12.03	23.11						
IL	2.77	3.92	-8.00	17.13	-35.28	-24.19	-47.30					
NT	**71.63**	72.78*	60.86*	**85.99**	33.59	44.67*	21.56	**68.86**				
Ip	**90.96**	**92.12**	**80.20**	**105.32**	52.92*	64.01*	40.90	**88.20**	19.33			
Ti	53.53*	54.69*	42.77*	**67.90**	15.49	26.58	3.47	50.77*	-18.10	-37.43*		
PRH	41.93*	43.08	31.16	56.29*	3.89	14.97	-8.14	39.16	-29.70	-49.04*	-11.61	
Pu	58.31*	59.46*	47.54*	72.67*	20.26	31.35	8.24	55.54*	-13.32	-32.66	4.77	16.38

Table 4.7: Pairwise comparisons for heterogeneity 3x3 (*$HAsfc_9$*).

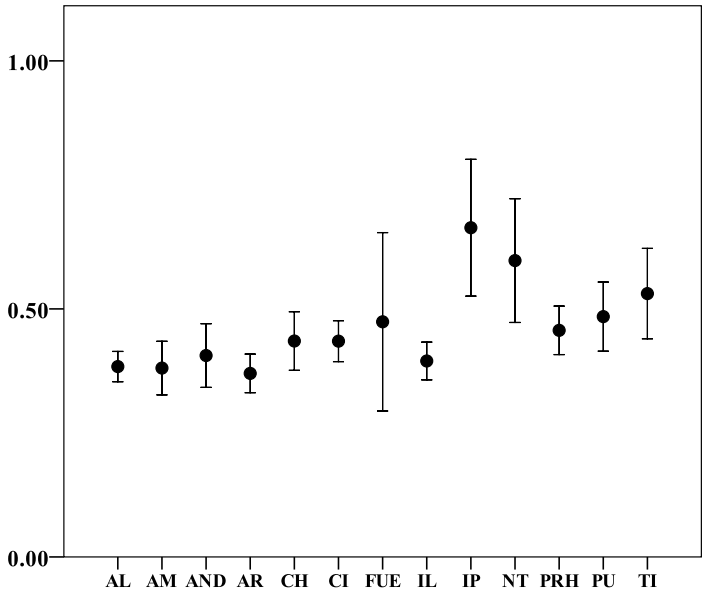


Figure 4.6: Box-and-whisker plots of heterogeneity 3x3 (*$HAsfc_9$*) by sample.

Al=Aleut; Am=Amarna; And=Andamanese; Ar=Arikara; CI=Chinese immigrants; Ch=Chumash; Fu=Fuegian; IL=Illinois Bluff; NT=Nunavut Territory Sadlermiut; Ip=Ipiutak; Ti=Tigara; PRH=Prince Rupert Harbour Tsimshian; Pu=Puye Pueblo.

Tukey's HSD pairwise comparisons indicate that the Ipiutak sample is significantly higher in *$HAsfc_9$* than the Aleut, Arikara, Illinois Bluff, Amarna, and

Andamanese. Moreover, the Fisher's LSD comparisons suggest this high-arctic sample has marginally higher heterogeneity 3x3 values than the Chinese immigrants, Tigara, Chumash, and Prince Rupert Harbour groups. The Nunavut Territory sample has significantly higher values than the Aleut, Arikara, and Illinois Bluff and marginally higher values than the Amarna, Andamanese, and Chumash samples. On a rather similar note, the Tigara is only significantly higher than the Arikara, but marginally higher than the Aleut, Illinois Bluff, Amarna, and Andamanese samples.

The Puye sample is marginally higher than five other groups, including the Aleut, Arikara, Illinois Bluff, Amarna, and Andamanese. The Prince Rupert Harbour also demonstrates marginally higher heterogeneity 3x3 values than the Aleut and Arikara. Lastly, the Chinese immigrants are marginally higher than the Arikara sample.

Heterogeneity 9x9 ($HAsfc_{81}$)

MATRICES OF PAIRWISE DIFFERENCES: HETEROGENEITY 9X9 (*HAsfc* $_{81}$)												
	Al	Am	And	Ar	CI	Ch	Fu	IL	NT	Ip	Ti	PRH
Am	-2.97											
And	-12.66	-9.69										
Ar	-20.68	-17.71	-8.02									
CI	20.30	23.27	32.96	40.98								
Ch	11.58	14.55	24.24	32.26	-8.73							
Fu	42.51	45.48	55.17	63.19*	22.21	30.93						
IL	-16.79	-13.82	-4.13	3.89	-37.09	-28.37	-59.30					
NT	**102.36**	**105.33**	**115.01**	**123.04**	**82.05**	**90.78**	59.85	**119.15**				
Ip	**102.03**	**104.00**	**114.68**	**122.71**	**81.72**	**90.45**	59.52	**118.82**	-0.33			
Ti	52.94*	55.91*	**65.60**	**73.62**	32.64	41.37*	10.44	**69.74**	-49.41*	-49.08*		
PRH	31.41	34.38	44.07*	52.09*	11.11	19.83	-11.10	48.20*	**-70.95**	**-70.62**	-21.54	
Pu	33.84	36.82	46.51*	54.53*	13.55	22.27	-8.66	50.64*	**-68.51**	**-68.18**	-19.10	2.43

Table 4.8: Pairwise comparisons for heterogeneity 9x9 ($HAsfc_{81}$).

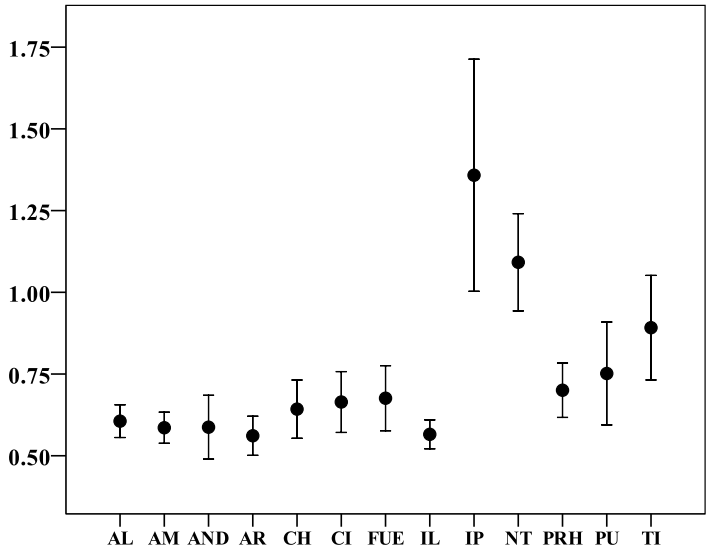


Figure 4.7: Box-and-whisker plots of heterogeneity 9x9 (*HAsfc*$_{81}$) by sample.

Al=Aleut; Am=Amarna; And=Andamanese; Ar=Arikara; CI=Chinese immigrants; Ch=Chumash; Fu=Fuegian; IL=Illinois Bluff; NT=Nunavut Territory Sadlermiut; Ip=Ipiutak; Ti=Tigara; PRH=Prince Rupert Harbour Tsimshian; Pu=Puye Pueblo.

Tukey's HSD and Fisher's LSD pairwise comparisons reveal that the Ipiutak and Nunavut Territory samples demonstrate the same results. They are both significantly higher in *HAsfc*$_{81}$ values than nine other samples, including the Aleut, Arikara, Chinese immigrants, Illinois Bluff, Puye, Amarna, Andamanese, Chumash, and Prince Rupert Harbour. Both are also marginally higher than the Tigara sample. These similar results are not unexpected considering the comparable high values, with the Ipiutak mean being 1.36 and the Nunavut Territory mean calculated at 1.09. The next highest mean value, 0.89, is that of the Tigara sample.

The Tigara sample is significantly higher in heterogeneity 9x9 values than the Arikara, Illinois Bluff, and Andamanese, and marginally higher than the Aleut, Amarna, and Chumash groups. Both the Prince Rupert Harbour and Puye samples are marginally

higher than the Arikara, Illinois Bluff, and Andamanese, while the Fuegians are marginally higher than the Arikara.

Discussion

These data provide additional evidence that bioarchaeological samples can be distinguished by their incisor microwear textures. In previous analyses, three texture variables, anisotropy (*epLsar*), textural fill volume (*Tfv*), and heterogeneity 3x3 ($HAsfc_9$), showed significant differences among five of the groups presented here: Aleut, Arikara, Chinese immigrants, Illinois Bluff, and Puye (Krueger & Ungar, 2010). Eight other bioarchaeological samples are added, resulting in significant differences in all five texture attributes.

In order to interpret the results, each texture attribute is discussed individually. Those variables that are significantly different in Krueger & Ungar (2010), anisotropy, textural fill volume, and heterogeneity 3x3, are discussed first, and the hypotheses generated from that study are supported or revised. Initial hypotheses are then produced for those texture attributes that are newly significant here, complexity, scale of maximum complexity, and heterogeneity 9x9. Only the hypotheses produced in Krueger and Ungar (2010) and supported here are used to explain microwear patterns and infer dietary and behavioral strategies in the fossil samples, following the criteria set forth for the comparative method (Kay & Cartmill, 1977; Anthony & Kay, 1993). Those hypotheses initially developed here for the modern human samples are used to only *suggest* possible explanations for the microwear patterns, but any explanations are considered preliminary and speculative pending further analyses.

Anisotropy (epLsar)

Past research shows anisotropy values to be low in those bioarchaeological groups that participated in non-dietary anterior tooth use behaviors (Krueger and Ungar, 2010). The interpretation for this trend is differences in the manner and/or frequency in which abrasives are dragged across the labial surfaces of the anterior teeth (Krueger and Ungar, 2010). Specifically, high anisotropy values on the labial surfaces of the anterior teeth would indicate abrasives being dragged apicocervically, as would be expected during the incising of food items. However, low anisotropy values, or a lack of feature directionality across the labial surface, would suggest the anterior teeth were being used in a variety of tasks that likely included non-dietary anterior tooth use.

Non-dietary anterior tooth use behaviors encompass a range of activities, but are most often associated with Alaskan Eskimo or Canadian and Greenland Inuit populations who used their anterior teeth as a tool, clamp, or third hand. Primarily reported by European and American explorers of the 19th century, both men and women were documented using their anterior teeth in activities such as hide preparation and softening and sinew thread production (Beechey, 1831; Simpson, 1875; Giffen, 1930; Moorrees, 1957; Burch, 1981; Foote, 1992).

Caribou was the most coveted animal for the production of clothing, boots, and sinew thread due to its warmth and durability; however, availability of this resource was both seasonal and limited in most areas, and hide tanning and preparation were arduous tasks, taking several weeks to complete (Gerlach, 1989; Foote, 1992). Other forms of non-dietary anterior tooth use have also been documented, including preparing and

softening fibers for basketry tasks (Cybulski, 1974), labret use (Cybulski, 1974; Lukacs & Pastor, 1987), and tool retouching (Man, 1883; Mayes, 2001).

The anisotropy results for the thirteen bioarchaeological samples examined here provide further support for the original interpretation presented in Krueger and Ungar (2010). Indeed, seven of the thirteen samples are reported to have participated in various forms of non-dietary anterior tooth use, including the Aleut, Illinois Bluff, Ipiutak, Tigara, Andamanese, Nunavut Territory, and Prince Rupert Harbour groups. All of these samples present low mean and median anisotropy values, garnering support for this variable being indicative of non-dietary anterior tooth use, and supporting the initial hypothesis put forth by Krueger and Ungar (2010).

The Ipiutak and Nunavut Territory samples demonstrate the greatest number of significant and marginally significant differences among the groups. Indeed, their anisotropy mean values are not only nearly identical, but also the lowest of all the samples (0.0020). The indistinguishable, extremely low values suggest these groups were participating in similar non-dietary anterior tooth use behaviors. Heavy caribou exploitation has been identified for both of these samples, and perhaps the low anisotropy values can be correlated to intense utilization of caribou hides and sinew for the production of clothing, boots, thread, and boat skins (Larsen and Rainey, 1948; Coltrain et al., 2004, Coltrain, 2009).

The Prince Rupert Harbour sample also show many significant and marginally significant differences, although not to the extent of the Ipiutak and Nunavut Territory. These individuals have been ethnographically documented wearing labrets and also using

the anterior teeth in basketry production. The low anisotropy values for this sample may relate to these forms of non-dietary anterior tooth use.

Interestingly, the remaining two arctic samples, the Aleut and Tigara, are both documented to have participated in heavy use of the anterior teeth in activities other than incising food items (Beechey, 1831; Hrdlička, 1945; Larsen and Rainey, 1948; Moorrees, 1957; Merbs, 1968; Foote, 1992). While overall these two samples have low anisotropy mean values (0.0030 and 0.0032), they have the highest two values of the seven samples proposed to utilize non-dietary anterior tooth use. Both groups are recorded as having limited exposure to caribou resources, and thus, would not have participated in the same intense clamping and grasping activities as that of the Ipiutak and Nunavut Territory populations. Their anisotropy values may reflect these limited behaviors; however, continued work will most likely help to identify the specific behaviors that can be attributed to these anisotropy values.

Lastly, the Illinois Bluff and Andamanese are both documented as participating in non-dietary anterior tooth use behaviors, and were marginally lower in anisotropy values than several other samples. These two groups are documented as using their anterior teeth in tool softening and retouching, so their low values may be due to these activities.

Textural fill volume (Tfv)

Previous incisor microwear texture research has tentatively associated textural fill volume with the amount and magnitude of repetitive loading of the anterior teeth or abrasive particle density or size, depending on whether the sample participated in non-dietary or dietary anterior tooth use behaviors (Krueger and Ungar, 2010). That is,

textural fill volume is attributed to the amount and magnitude of anterior tooth loading if the modern human sample participated in non-dietary anterior tooth use behaviors (signaled by low anisotropy values, see above). This hypothesis was generated in Krueger & Ungar (2010), and built on the premise that non-dietary anterior tooth use behaviors, usually associated with clamping and grasping hide preparation activities, require the production of heavy and continuous force on the anterior dentition in order to perform these tasks (Spencer & Demes, 1993; Ungar & Spencer, 1999; Spencer & Ungar, 2000). This heavy and continuous force would be applied to grit- and fur-laden hides, creating microwear textures high in textural fill volume.

On the other hand, textural fill volume is recognized as an indicator of abrasive particle density or size if the modern human sample participated only in dietary anterior tooth use (signaled by high anisotropy values, see above). This hypothesis was put forth in Krueger & Ungar (2010), and developed from the idea that dietary use of the anterior dentition would produce microwear features associated with food fracture properties or, more congruent with the function of the anterior dentition, adherent abrasives on food items. Therefore, high textural fill volume values may indicate high abrasive density or large-sized abrasives, and vice versa.

The Nunavut Territory and Ipiutak samples show significantly higher textural fill volume values than every other group other than the Fuegians. These two high-arctic samples are also significantly or marginally lower in anisotropy than all other groups except the Prince Rupert Harbour sample. The combination of extremely low anisotropy and exceptionally high textural fill volume, along with nearly identical values in both

texture attributes, suggest these two groups were similar in their intense anterior tooth use.

As described in Chapter 3, the Ipiutak were seasonal occupants of Point Hope, following the migration patterns of the caribou herds and relying predominantly on them for subsistence (Larsen and Rainey, 1948). Likewise, the Nunavut Territory Sadlermiut also relied heavily on caribou, with the stable isotope data confirming the ethnographic record (Coltrain et al., 2004; Coltrain, 2009). Thus, it seems plausible that the combination of extremely low values in anisotropy and exceptionally high values in textural fill volume could be related to a heavy regimen of caribou hide and sinew preparation and utilization for not only themselves, but for trade with coastal whaling communities. This intense clamping and grasping regimen would have required the production of heavy and continuous force on the anterior dentition, producing the extremely high textural fill volume values.

The Prince Rupert Harbour sample also indicates anterior tooth use behaviors with low anisotropy values; however, the textural fill volume does not support the same clamping and grasping tooth use behaviors as those associated with the high-arctic samples. The textural fill volume is only significantly higher than the Illinois Bluff and Andamanese and marginally higher than the Arikara and Amarna samples. Indeed, these results hint at the moderate *Tfv* mean value of 5766 for the Prince Rupert Harbour collection. The combined low anisotropy value and moderate textural fill volume provides support for non-dietary anterior tooth use without high magnitude or repetitive loading of the anterior teeth. Previous analyses suggest this group wore lip labrets and also used their anterior teeth in preparing fibers for basketry production, neither of which

would have required high magnitude or repetitive loading of the anterior teeth (Cybulski, 1974). Therefore, it is suggested that the Prince Rupert Harbour microwear texture data provide additional evidence for these behaviors.

The Tigara and Aleut also demonstrate low anisotropy values that are marginally lower than the Puye. Although, as described above, these two samples demonstrate the highest *epLsar* mean values of the non-dietary anterior tooth use samples, they are ethnographically documented as using their anterior teeth in behaviors other than incising food items (Beechey, 1831; Simpson, 1875; Giffen, 1930; Hrdlička, 1945; Moorrees, 1957; Foote, 1992). Both the Tigara and Aleut textural fill volume values are intermediate between the extremely high Nunavut Territory and Ipiutak and the moderate Prince Rupert Harbour values. As a result, these data suggest that these two groups used their anterior dentition in similar ways.

The Tigara (Taraeumiut) resided at Point Hope on a year-round basis, and relied predominantly on whale hunting, supplemented by other sea mammals such as walrus and seal (Larsen and Rainey, 1948; Foote, 1992). Birds, fish, berries, and other edible plants, when available, were also consumed (Foote, 1992). The caribou and whale migration patterns changed from the Ipiutak to Tigara occupations, so whale and other sea mammals were readily available, but caribou often was not (Gerlach, 1989; Foote, 1992) However, because caribou was coveted for its warmth and durability, their skins were traded by interior Nunamiut groups in exchange for fuel in the form of whale blubber (Andrews, 1939; Gubser, 1965; Burch, 1981; Foote, 1992).

The Aleut, excavated from various Aleutian Islands, relied on sea resources such as raw and dried fish and sea mammals, but also took small land mammals (Hrdlička,

1945; Moorrees, 1957; Hoffman, 1993; Coltrain, 2010). Both the Tigara and Aleut would not have had the means or opportunity to exploit the caribou resources as heavily as the Nunavut Territory and Ipiutak groups, and most likely obtained the coveted caribou from the interior populations through trade. Sea mammals, such as walrus and seal, were utilized, but the skins were not heavily scraped or softened in order to maintain stiffness, and bladders, intestines, and stomachs were used for containers, waterproof boots, and floats (see Foote, 1992 for a very detailed explanation of butchering and sewing techniques). Moreover, at least for the Tigara, alternative hide processing techniques that use a foot as a third hand instead of the anterior dentition, are documented (Foote, 1992:65). For these reasons, the Tigara and Aleut would not have required the production of heavy and continuous force on the anterior dentition as that of the Ipiutak and Nunavut Territory samples. Therefore, the moderately high textural fill volume values support the moderately heavy use of the anterior dentition in clamping and grasping activities.

The Illinois Bluff and Andamanese, the remaining samples that are documented as using non-dietary anterior tooth use, also demonstrate low *epLsar* values. However, the Illinois Bluff *Tfv* values are one of the lowest of the samples, and the Andamanese is the lowest value of all the groups. The combination of low anisotropy and low textural fill volume values of both of these samples may indicate non-dietary anterior tooth use, but in a manner that did not at all require high magnitude or repetitive loading.

Ethnographic reports describe the Andamanese softening and retouching arrow points with their anterior teeth, while analyses of the Illinois Bluff sample suggests tool retouching as the reason for the chipping found on the anterior dentition (Man, 1885;

Mayes, 2001). Stone tool softening or retouching would have required small areas of compression for small fragments to be removed, not high magnitude loading of the anterior teeth. Consequently, it is unsurprising, given these ethnographic descriptions, that the Andamanese and Illinois Bluff samples have low anisotropy and textural fill volume values.

The original hypothesis generated by Krueger & Ungar (2010) indicated that textural fill volume values of samples with non-dietary anterior tooth use behaviors signal the amount and magnitude of anterior tooth loading. The data presented here presents a convincing argument for this association, and the expansion of the original five samples to thirteen continues to support this initial hypothesis.

The remaining six bioarchaeological samples, including the Fuegian, Chumash, Puye, Chinese immigrants, Amarna, and Arikara, all have anisotropy values indicative of primarily using the anterior dentition for incising food items, and most likely did not participate in non-dietary anterior tooth use and high magnitude or heavy loading of the anterior teeth. However, the original hypothesis posited in Krueger & Ungar (2010) supports textural fill volume data of these samples as a potentially useful proxy for abrasive particle density or size, and the addition of eight samples will either maintain or refute this hypothesis.

The Fuegian sample has the highest textural fill volume of these samples, with a mean value of 9151. As described above, this sample has significantly higher fill volume values than the Illinois Bluff and Andamanese, and marginally higher values than the Arikara, Chinese immigrants, and Amarna samples. The Fuegians relied predominantly on marine resources, such as seals, sea lions, and fish, and heavy winds are reported

along these subsistence areas, exposing them to different types and sizes of both dietary and wind-borne abrasives (Yesner et al., 2003). Similarly, the high *Tfv* value found in this sample indicates high exposure to a variety of abrasive types; however, the sample size is meager, and these interpretations are extremely speculative.

The Chumash and Puye represent groups of moderate *Tfv* values; however, both produced significant and/or marginally significant results. While the Chumash was significantly higher and the Puye was marginally higher than the Illinois Bluff, both the Chumash and Puye were marginally higher than the Arikara, Amarna, and Andamanese samples.

The Chumash lived on the Channel Islands off the coast of southern California, and the landscape consisted of sand beaches and cliff landscapes with minimal vegetation cover and high surf (Van Valkenburgh, 1933). They relied almost entirely on marine resources, such as abalone, seals, and mollusks, and abrasives, such as sand, came into contact with these food items during ingestion. The Puye, on the other hand, lived on the open Pajarito Plateau in the desert climate of New Mexico, and relied mainly on crops such as maize, beans, and squash (Hewett, 1938; Barnes, 1994). Not only were phytoliths present in maize and other plants, but the utilization of the mano and matate grinding system introduced stone abrasives into the meal. The open, arid landscapes of these two areas, as well as subsistence strategies employed by these two groups identifies contact with a variety of environmental and/or dietary abrasive types. Congruently, both these samples had similar, moderate *Tfv* values.

Lastly, the Chinese immigrants, Amarna, and Arikara samples were not significantly or marginally higher in *Tfv* than any other group, and represent the lowest

fill volume values of all the bioarchaeological groups analyzed here. The Chinese immigrants had the highest value of these three, and their location on the coast of Kodiak Island and/or employment at the Karluk Fish Cannery may account for some contact with environmental or dietary abrasives. There is only marginal information about diet and lifestyle of these individuals, so these data are speculative at best.

The extremely low values for the Amarna and Arikara samples are surprising considering the former is a desert site and the latter relied on bison meat dried on racks in the open landscape. Perhaps they came into contact with limited types and/or small sizes of abrasives, and perhaps their minimal *Tfv* values reflect this kind of exposure; however, it might also indicate, at least with the Amarna sample, the consumption of foods high in elasticity. That is, perhaps the main dietary staple was extremely soft, and did not require much incisal preparation to consume. Molar microwear texture analysis would complement these data here, and provide insight into the dietary and abrasive loads of the Amarna sample.

It is clear from these last three samples that the association between dietary anterior tooth use, textural fill volume values, and abrasive particle density or size is not as straightforward as originally presented in Krueger & Ungar (2010). While this association seems to be buttressed by the majority of samples, the Chinese, Amarna, and Arikara samples are not compatible with it. Perhaps, as mentioned for the Amarna sample, food properties themselves are affecting textural fill volume values, and are either exacerbating or reducing the signal. Continued analyses will allow for further testing.

Heterogeneity 3x3 (HAsfc9)

Significant differences in heterogeneity 3x3 have been linked to not only the level of abrasive exposure, but also the variability in size of abrasive particles (Krueger and Ungar, 2010). This was taken from the idea that the presence of a variety of abrasive types and sizes, either wind-borne or adherent on food items during incising, would leave a variety of differently sized microwear features, creating high variability of textures across the enamel surface (Krueger & Ungar, 2010).

As with the textural fill volume values, the Ipiutak and Nunavut Territory samples demonstrate significantly or at least marginally higher values than the majority of other groups. Both of these samples are coastal, and were exposed to high amounts of sand and other wind-borne abrasives; however, this cannot account for the high heterogeneity values in and of themselves. Many of the other samples are also coastal and would have been exposed to the same types and amounts of abrasives, but do not display the same high heterogeneity 3x3 values as these two groups. As a result, perhaps the uniquely intense non-dietary anterior tooth use behaviors suggested for these groups are also playing a role in the high variation of microwear textures.

This idea is strengthened by the significant and marginally significant results of the Tigara sample. They do not demonstrate the highest value overall, but their practice of non-dietary anterior tooth use coupled with the fairly high heterogeneity 3x3 values supports the idea that these behaviors influence this texture attribute. Further confirmation is found with the marginally higher values of the Prince Rupert Harbour sample. While this group did participate in non-dietary anterior tooth use behaviors, they

were not as intense and did not require the high magnitude loading as those of the Ipiutak and Nunavut Territory samples.

The other significant differences are found in samples that did not engage in non-dietary anterior tooth use behaviors, and they support the original hypothesis presented in Krueger & Ungar (2010), namely, that they are exclusively due to variability in abrasive exposure. The Puye sample is marginally higher than five other groups, and their recorded high exposure to phytoliths, sand, and stone grinding abrasives suggest intense contact with various types of dietary and environmental abrasives. Lastly, the Chinese immigrants are marginally higher than the Arikara sample, and this may simply reflect some exposure to abrasives. This is strengthened when the lower textural fill volume of the Chinese sample is also considered, but this idea remains speculative.

These datasets allows for a slight revision to the original hypothesis from Krueger & Ungar (2010), in which heterogeneity 3x3 was suggested to indicate only the level of abrasive exposure and the variability in size of abrasive particles. The expanded dataset suggest that the heterogeneity 3x3 texture attribute reflects only abrasives in those samples that participate in dietary use of the anterior dentition. On the other hand, these data indicate that the heterogeneity 3x3 signal is exacerbated in those samples that used their anterior dentition in non-dietary activities. Further analyses will be required to strengthen this revised hypothesis.

Heterogeneity 9x9 (HAsfc81)

Heterogeneity 9x9 did not demonstrate significant differences in previous analyses by Krueger & Ungar (2010); however, the addition of eight samples results in

statistically significant differences. Therefore, a new hypothesis must be generated for these significant results, and exploratory interpretations presented. Since heterogeneity 9x9 is the fine-scale variant of heterogeneity 3x3, a parsimonious preliminary hypothesis for the 9x9 significant results would be similar to that found for the 3x3 results. Therefore, it would be predicted that those samples with dietary anterior tooth use only would have microwear texture variability indicative only of abrasive loads. On the other hand, those with non-dietary anterior tooth use behaviors may have elevated microwear texture variability than would be predicted from the abrasive exposure alone.

Four of the five arctic samples, including the Ipiutak, Nunavut Territory, Tigara, and Prince Rupert Harbour samples show significantly or marginally higher $HAsfc_{81}$ values. Keeping in line with the other texture variables, the Ipiutak and Nunavut Territory are significantly higher in heterogeneity 9x9 than nine other samples and marginally higher than the Tigara. The Tigara and Prince Rupert Harbour also demonstrate higher values, although the differences are not as numerous as the Ipiutak and Nunavut Territory.

These results not only support the revised hypothesis for heterogeneity 3x3, but also the new hypothesis for 9x9, in which non-dietary anterior tooth use increases variability in microwear textures, resulting in higher-than-predicted heterogeneity 9x9 values based upon abrasive exposure alone. Moreover, the range of values of the arctic samples suggests this texture attribute can also signal the intensity of tooth use behaviors.

For those samples that participated in dietary use of the anterior dentition, the hypothesis predicts the heterogeneity 9x9 values indicate abrasive exposure alone. The Puye sample is marginally higher than the Arikara, Illinois Bluff, and Andamanese, while

the Fuegians are marginally higher than the Arikara. The Puye results reflect the same signal as that of heterogeneity 3x3, which most likely reflect their high exposure to different types of environmental and dietary abrasives. The marginally significant result of the Fuegian sample also supports the coastal and wind-borne environment of this population.

Complexity (Asfc)

The complexity variable has been an especially useful indicator of hard object feeding in extant and extinct primate and hominin molar microwear texture studies (Ungar et al., 2003; Scott et al., 2006; Krueger et al., 2008; Ungar et al., 2008a; Ungar et al., 2008b; Scott et al., 2009). Previous analyses of incisor microwear texture complexity did not yield significant variation among the groups, but differences are found when the additional samples are added.

The complexity variable measures changes in surface roughness with the scale of observation. It seemed plausible that for incisor textures, the complexity values may correlate with heterogeneity, which, as mentioned above, is a measure of texture variation across the enamel surface. That is, high heterogeneity values correspond to differently sized features across the enamel surface, and these variably sized features could correspond to increased changes in surface roughness. When the mean complexity values for each sample were plotted along with the heterogeneity 3x3 mean values, a general correlation was found. That is, when complexity increases, heterogeneity also increases, and, conversely, when complexity values decrease, the heterogeneity values

also decrease. Moreover, the fine-scale heterogeneity variants, such as heterogeneity 9x9 10x10, and 11x11, plotted even more precisely than those of the coarse scales (Fig. 4.3).

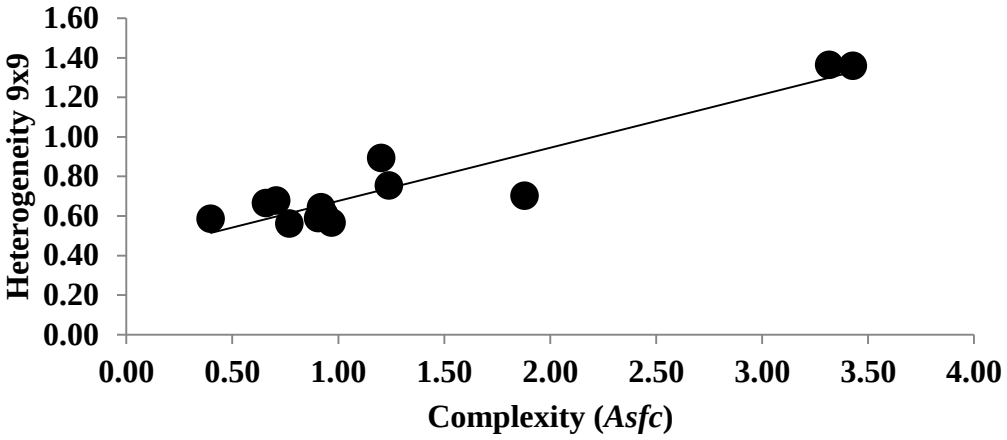


Figure 4.8: Plot of the mean complexity (*Asfc*) and heterogeneity 9x9 ($HAsfc_{81}$) values for each modern human sample.

In order to assess whether these variables are correlated, a Spearman correlation was performed on ranked *Asfc* and $HAsfc_{81}$ mean data for all thirteen samples (Madrigal, 1998). The Spearman correlation coefficient is 0.691, which indicates a marginally strong, positive correlation[13]. This correlation was significant at the 0.01 level (Table 4.9).

		Rank of *Asfc*	Rank of $HAsfc_{81}$
Rank of *Asfc*	Spearman Correlation	1	0.691
	Sig. (2-tailed)		0.009
	N		13

Table 4.9: Spearman correlation results between complexity (*Asfc*) and heterogeneity 9x9 ($HAsfc_{81}$) means for the 13 samples.

[13] A coefficient value over 0.80 is considered strongly correlated. A positive number indicates a positive correlation, whereas a negative number denotes a negative correlation. The closer to +1 (or -1), the stronger the positive (or negative) correlation (Madrigal, 1998).

Consequently, if the complexity variable is positively correlated to heterogeneity, then perhaps this texture attribute can be tentatively interpreted as differences in surface roughness in relation to two factors: 1. the level of exposure to different sizes and types of dietary and/or environmental abrasives and 2. the level of non-dietary anterior tooth use. If a group is both exposed to high amounts of abrasives and employed anterior tooth use behaviors, their complexity values may be exceedingly high. The fact that the Ipiutak and Nunavut Territory samples represent the largest values and, consequently, the most significant and marginally significant outcomes provides evidence for this initial interpretation.

Further, the Prince Rupert Harbour complexity results show the same number of significant differences as the Ipiutak and Nunavut Territory groups, even though the mean *Asfc* value is lower than the other two arctic groups. Regardless, these three samples employed non-dietary anterior tooth use and lived in areas where exposure to abrasive loads is predicted to be high. Further, the Tigara sample shows marginally higher complexity values than the Chinese immigrants and Arikara; these results reflect the moderate non-dietary anterior tooth use and moderately high heterogeneity values found in this group.

The Illinois Bluff and Puye samples are marginally higher in complexity than the Chinese immigrant group. These results may suggest that *moderate* surface roughness can manifest from *either* non-dietary anterior tooth use or high abrasive loads. The Illinois Bluff sample demonstrates low heterogeneity and anisotropy values, suggesting low abrasive loads, but non-dietary anterior tooth use in the form of tool retouching. This behavioral repertoire may have resulted in their moderate complexity values. On the

other hand, the Puye demonstrate high heterogeneity and anisotropy values, indicating high abrasive loads, but no dietary anterior tooth use. This condition may have lead to the moderate complexity values seen in this analysis, although these interpretations should be taken as speculative and preliminary.

Lastly, the extremely low complexity value of the Amarna sample can reveal important clues concerning the proposed dietary and behavioral strategies of this New Kingdom Egyptian group. This sample is significantly or marginally lower in its complexity values than the Aleut, Arikara, Illinois Bluff, Puye, Ipiutak, Tigara, Andamanese, Chumash, Nunavut Territory, and Prince Rupert Harbour samples. The extremely low complexity, high anisotropy, and low heterogeneity values suggest this group did not participate in non-dietary anterior tooth use behaviors, high magnitude or heavy loading of the anterior tooth, and were exposed to low amounts of large or variably-sized dietary or environmental abrasives.

Scale of maximum complexity (Smc)

The scale of maximum complexity provides information concerning the scale at which the majority of features are found. Larger features are expected to result in higher *Smc* values, and vice versa (Scott et al., 2006). The Fuegian sample had the highest *Smc* mean value, and this is reflected in the number of significant and marginally significant outcomes. This suggests the Fuegian sample displayed the most features at a very coarse scale; however, the sample size is small, and these results are speculative.

The Amarna sample was significantly or marginally higher than the majority of the other samples. The high *Smc* coupled with the values of the other Amarna texture

attributes suggest few, shallow, and large features on the enamel surface. Additionally, *Smc* is the only variable by which the Nunavut Territory and Ipiutak samples can be distinguished. In fact, while the Nunavut Territory has one of the highest mean values, the Ipiutak has one of the lowest, along with the Puye and Illinois Bluff samples. In fact, the Prince Rupert Harbour sample is also marginally higher than both the Ipiutak and Puye samples, and the Tigara demonstrates a marginally higher result than that of the Ipiutak. This suggests that while the Ipiutak has the lowest anisotropy and highest complexity, textural fill volume, and heterogeneity values, the majority of their features are found at a fine scale. The interpretation of *Smc* and its importance in distinguishing groups by their incisor microwear textures is in the early stages, and further analyses may shed light on the functional implications of these differences.

Conclusion

These data provide further evidence for the usefulness of incisor microwear texture analysis in distinguishing between bioarchaeological samples with different dietary strategies, forms of non-dietary anterior tooth use behaviors, and dietary and environmental abrasive load exposure, type, and size. Although the initial analyses only found significant differences in anisotropy, textural fill volume, and heterogeneity 3x3, the addition of several other samples adds complexity, scale of maximum complexity, and heterogeneity 9x9 to the list of significantly different texture attributes.

The addition of a wide variety of samples, including several arctic, tropical, and desert groups, allows for a finer-scale assessment, and the combination of incisor texture attributes permits as much information as possible to be gleaned from the method at hand. For example, the seven samples documented to engage in non-dietary anterior

tooth use behaviors all had low anisotropy levels; however, the range of low anisotropy levels, from the lowest Ipiutak and Nunavut Territory samples to the higher Tigara values, along with the breadth of textural fill volume values, allows specific behaviors to be correlated to these values.

For example, both the Ipiutak and Nunavut Territory have extremely low anisotropy values and exceptionally high textural fill volume results. This is suggested to indicate specialized, frequent, and intense grasping, clamping, and manipulation of coveted caribou hides. On the other hand, the low anisotropy and moderate textural fill volume of the Prince Rupert Harbour sample is proposed to reflect both basketry production and lip labret use, which would not require high magnitude or repetitive loading of the anterior dentition. Conversely, those samples that demonstrate higher anisotropy values most likely did not employ non-dietary anterior tooth use behaviors, and the textural fill volume values may reflect abrasive particle density and size, although further testing is required.

Both variants of heterogeneity, $HAsfc_{9}$ and $HAsfc_{81}$, also seem to be indicators of dietary and/or environmental abrasives, and seem to suggest both level of exposure and variability in size, although those samples that participated in non-dietary anterior tooth use behaviors show higher heterogeneity values than the abrasive exposure would predict. Moreover, complexity is positively correlated with heterogeneity, and both values change in tandem for each group; that is, as the heterogeneity values increases, the complexity value also increases. However, the complexity value doesn't fluctuate as much as the heterogeneity value, which might be the reason why the Spearman

correlation coefficient wasn't extremely strong, and the complexity attribute did not show significant results in the preliminary analysis, while heterogeneity did.

Regardless, this correlation suggests these two texture attributes are linked, which makes sense given their definitions. As heterogeneity increases, it signals an increase in variability in textures across the enamel surface. This increase in variability would most likely result in added surface roughness, or complexity. Further research will no doubt shed light on this phenomenon. Lastly, the scale of maximum complexity allows for analysis of the fine-scale limit of complexity, or the scale at which the majority of features are found.

In conclusion, this study strongly supports incisor microwear texture analysis for indicating several important attributes of subsistence and behavioral strategies across a wide variety of populations. The interpretations of bioarchaeological groups are both significant and imperative for making inferences about fossil hominins, especially those with hypothesized application of non-dietary anterior tooth use behaviors. In the next chapter, these interpretations are used to build a framework of Neandertal behavior across time and space.

CHAPTER FIVE: NEANDERTALS

Results

Sixty-five adult Neandertal individuals preserve microwear texture signatures and are used in this study. These individuals date from OIS 7 to OIS 3, and extend over much of the range of the Neandertal distribution. The most northern individual included in this study is that from Pontnewydd in Wales, the most southern are those from several sites in Israel, the most eastern is from Shanidar in Iraq, and the most western is from Zafarraya in Spain (Fig. 5.1). The descriptive statistics for the entire Neandertal sample are presented in Table 5.1.

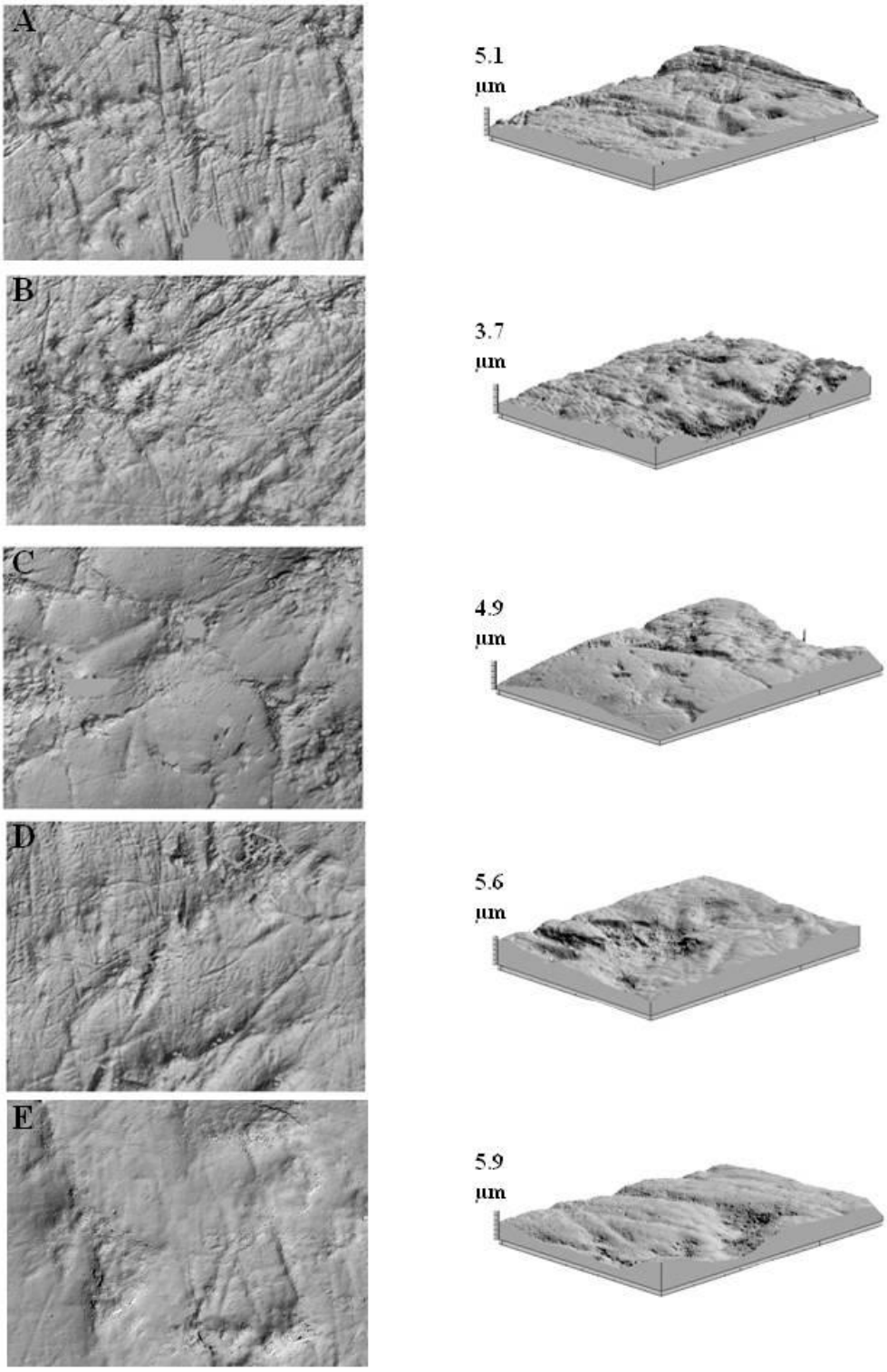
NEANDERTALS OVERALL						
	Asfc	***Smc***	***epLsar***	***Tfv***	***HAsfc9***	***HAsfc81***
Mean	1.18	9.19	0.0030	9149.93	0.47	0.76
Median	1.03	0.42	0.0028	9661.46	0.46	0.72
SD	0.72	40.23	0.0013	4762.57	0.12	0.24

Table 5.1: Descriptive statistics of the entire Neandertal sample, *n* = 65.

In order to expand the breadth of the study as much as possible, a variety of anterior tooth types, both maxillary and mandibular, are utilized in this study; however, it has been suggested that different anterior teeth may demonstrate significantly different microwear texture signals, and this hypothesis is tested first.

A two-factor multivariate analysis of variance (MANOVA) is performed on ranked microwear texture data in which tooth type (central incisors, lateral incisors, and canines) and jaw (maxilla and mandible) are presented as the factors, and the microwear texture attributes are the dependent variables. This statistical test shows no significant interaction between these two factors, or significant differences in microwear textures by tooth type or jaw (Table 5.2). This suggests that regardless of the specific anterior tooth type, position in the jaw, or jaw itself, the microwear signal remains constant. For the

first time, data support the inclusion of different anterior tooth types in microwear texture analysis.



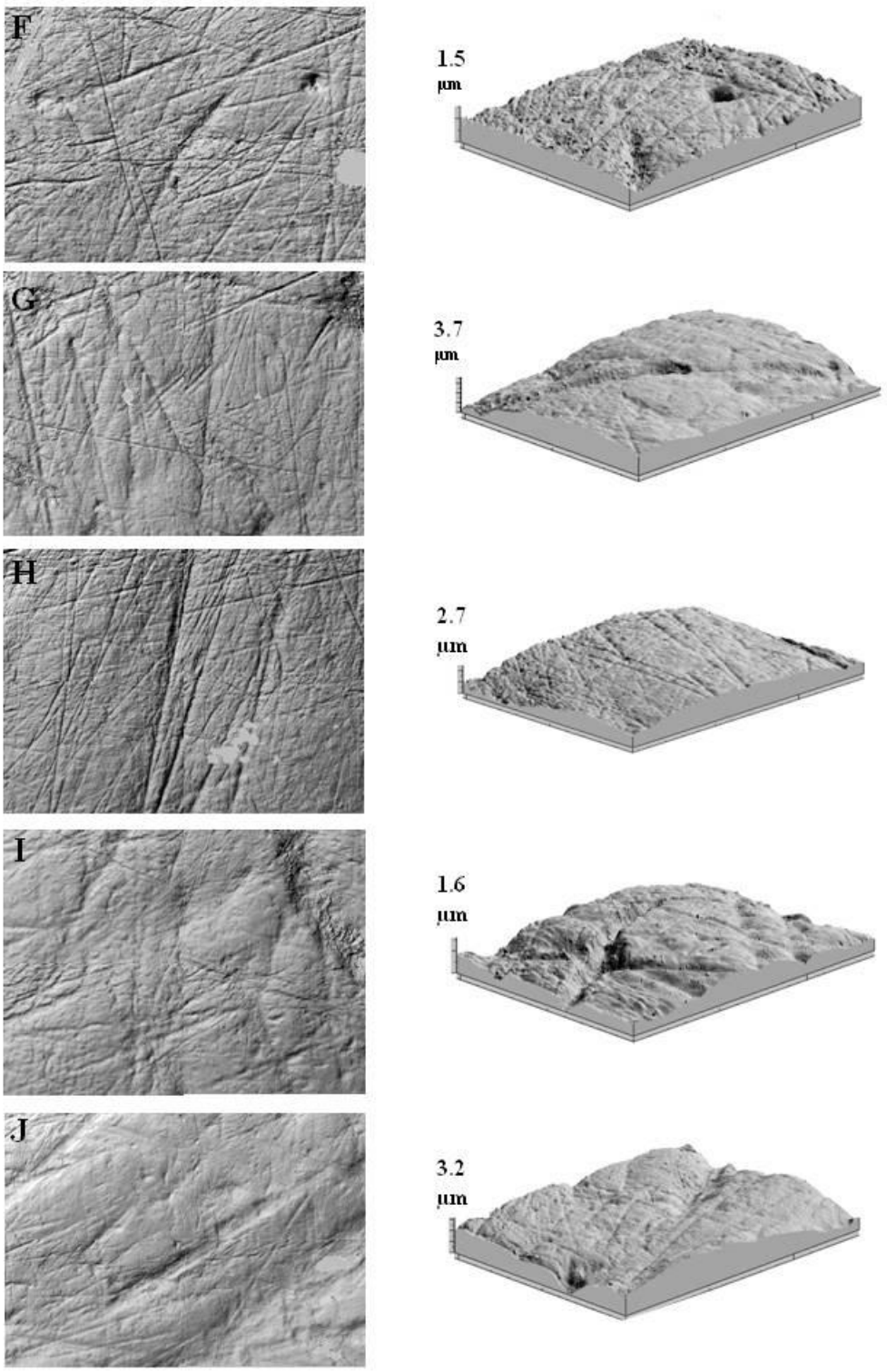


Figure 5.1: Point cloud examples of Neandertals

A=Biache-Saint-Vaast 1, **B**=Rochelot 1, **C**=La Ferrassie I, **D**=La Ferrassie II, **E**=Combe Grenal 5, **F**=Kebara 2, **G**=Krapina 73, **H**=Shanidar 3, **I**=Vindija 290, **J**=Zafarraya Z23.

MANOVA					
		Test statistic	***F***	**df**	***p***
Tooth Type	Pillai's Trace	0.09	0.43	12, 104	0.95
	Wilks' λ	0.91	0.42	12, 102	0.95
	Holtelling's Trace	0.10	0.42	12, 100	0.96
Jaw	Pillai's Trace	0.07	0.61	6, 51	0.72
	Wilks' λ	0.93	0.61	6, 51	0.72
	Holtelling's Trace	0.07	0.61	6, 51	0.72
Tooth Type * Jaw	Pillai's Trace	0.14	0.67	12, 104	0.78
	Wilks' λ	0.86	0.66	12, 102	0.79
	Holtelling's Trace	0.16	0.65	12, 100	0.79

Table 5.2: Results of the two-factor MANOVA testing differences in microwear textures between anterior tooth type and jaw. Analyses performed on ranked data.

Now that the lack of significant differences between tooth type and jaw is established, further statistical tests are warranted to determine more specific variation in texture signals among the Neandertal sample. First, Levene's Test of Equality of Error Variances is performed on raw data to determine homogeneity of variance. While there are no significant differences by location or OIS number, there are significant differences in anisotropy, scale of maximum complexity, and textural fill volume by climate (Table 5.4). This indicates there are differences in variance between the climate subcategories in these texture attributes.

Originally, a three-factor MANOVA was to be performed on ranked microwear texture data, with OIS number, climate, and location listed as the factors, and each texture attribute as a separate dependent variable. However, several of the OIS categories lacked a sufficient sample to justify their separation for the MANOVA test. Specifically, it is generally accepted that the sample size needs to be greater than the number of dependant variables, and individuals from OIS 7, 7/6, and 4/3 would have been excluded from all

analyses. Therefore, to retain the expanded sample size, a two-factor MANOVA, with climate and location as factors, and each texture attribute as dependent variables, is performed on ranked microwear texture data. Additionally, a MANOVA with OIS as the factor is run separately, and includes only those oxygen isotope stages with sufficient sample sizes, including OIS 6/5, 5, 4, and 3.

Significant differences in climate, location, and OIS are found, and individual analyses of variance (ANOVAs) for each texture attribute, as well as pairwise comparisons for the location and OIS factors, are calculated to find the sources of significant variation, as needed. There is no significant interaction between climate and location, but this outcome is not unexpected considering the changes in climate across the range of the Neandertal distribution. One would not expect climate and location to be intrinsically linked over such a long period of time, during which several extreme and moderate climatic oscillations occurred at any one given location. Interaction between factors aside, the results of each factor are described separately.

Climate

The descriptive statistics for the two climate categories, warm-woodland and cold-open-steppe environments, are found in Table 5.3. The Levene's test demonstrates significant differences between the two climate subcategories in the distribution variance (Table 5.4), while the two-factor MANOVA demonstrates suggestive significant differences in climate subcategories' central tendencies (Table 5.5). Indeed, the individual, two-factor ANOVAs indicate significant variation in anisotropy (*epLsar*) and textural fill volume (*Tfv*) in central tendencies and distribution variance of the two

climate categories (Table 5.6, Figure 5.2). Additionally, differences in the distribution variance for the scale of maximum complexity are also found. The central tendencies will be discussed first.

Since only two subcategories are used, pairwise comparisons tests are unnecessary for these two texture attributes. The significant variation in anisotropy central tendencies can be attributed to the extremely low *epLsar* values of the cold-open-steppe Neandertals. Indeed, the statistically significant difference can be interpreted from the means, with the cold-open-steppe and warm-woodland values at 0.0022 and 0.0033, respectively.

The significant difference in textural fill volume central tendencies can also be attributed to the cold-open-steppe Neandertals; however, this category's values are significantly higher than those found for the warm-woodland individuals. The mean values for the cold-open-steppe and warm-woodland Neandertals are 11,719 and 8,240, respectively.

NEANDERTALS BY CLIMATE: WARM-WOODLAND						
	Asfc	***Smc***	***epLsar***	***Tfv***	***HAsfc$_9$***	***HAsfc$_{81}$***
Mean	1.10	3.02	0.0033	8239.98	0.45	0.71
Median	0.99	0.42	0.0031	8760.78	0.45	0.67
SD	0.69	12.51	0.0013	4937.49	0.11	0.21
NEANDERTALS BY CLIMATE: COLD-OPEN-STEPPE						
	Asfc	***Smc***	***epLsar***	***Tfv***	***HAsfc$_9$***	***HAsfc$_{81}$***
Mean	1.41	26.62	0.0022	11719.20	0.54	0.91
Median	1.08	0.34	0.0019	12423.39	0.54	0.85
SD	0.80	74.69	0.0008	3101.25	0.14	0.26

Table 5.3: Descriptive statistics of the Neandertal sample by climate. Warm-woodland *n* = 48 and cold-open-steppe *n* = 17.

LEVENE'S TEST BY CLIMATE			
	F	**df**	***p***
Asfc	0.996	1, 63	0.32
epLsar	4.970	1, 63	0.03
Smc	18.317	1, 63	0.00
Tfv	4.957	1, 63	0.03
$HAsfc_9$	1.659	1, 63	0.20
$HAsfc_{81}$	2.174	1, 63	0.15

Table 5.4: Levene's Test results showing significant differences in variance by climate.

MANOVA					
		Test statistic	***F***	**df**	***p***
Climate	Pillai's Trace	0.18	1.99	6, 55	0.06
	Wilks' λ	0.82	1.99	6, 55	0.06
	Holtelling's Trace	0.22	1.99	6, 55	0.06
Location	Pillai's Trace	0.37	2.10	12, 112	0.02
	Wilks' λ	0.66	2.13	12, 110	0.02
	Holtelling's Trace	0.48	2.15	12, 108	0.02
Climate * Location	Pillai's Trace	0.09	0.87	6, 55	0.52
	Wilks' λ	0.91	0.87	6, 55	0.52
	Holtelling's Trace	0.10	0.87	6, 55	0.52

Table 5.5: Two-factor MANOVA with climate and location as factors. Analyses performed on ranked data.

ANOVAs				
	Sum of Squares	***F***	**df**	***p***
Asfc	143.68	0.446	1	0.507
epLsar	1484.524	4.685	1	0.034
Smc	9.301	0.026	1	0.872
Tfv	1404.494	4.285	1	0.043
HAsfc9	726.931	2.151	1	0.148
HAsfc81	73.241	0.252	1	0.618

Table 5.6: Climate results from two-factor ANOVAs on ranked data. Pairwise comparisons are unnecessary since only two climate categories were used.

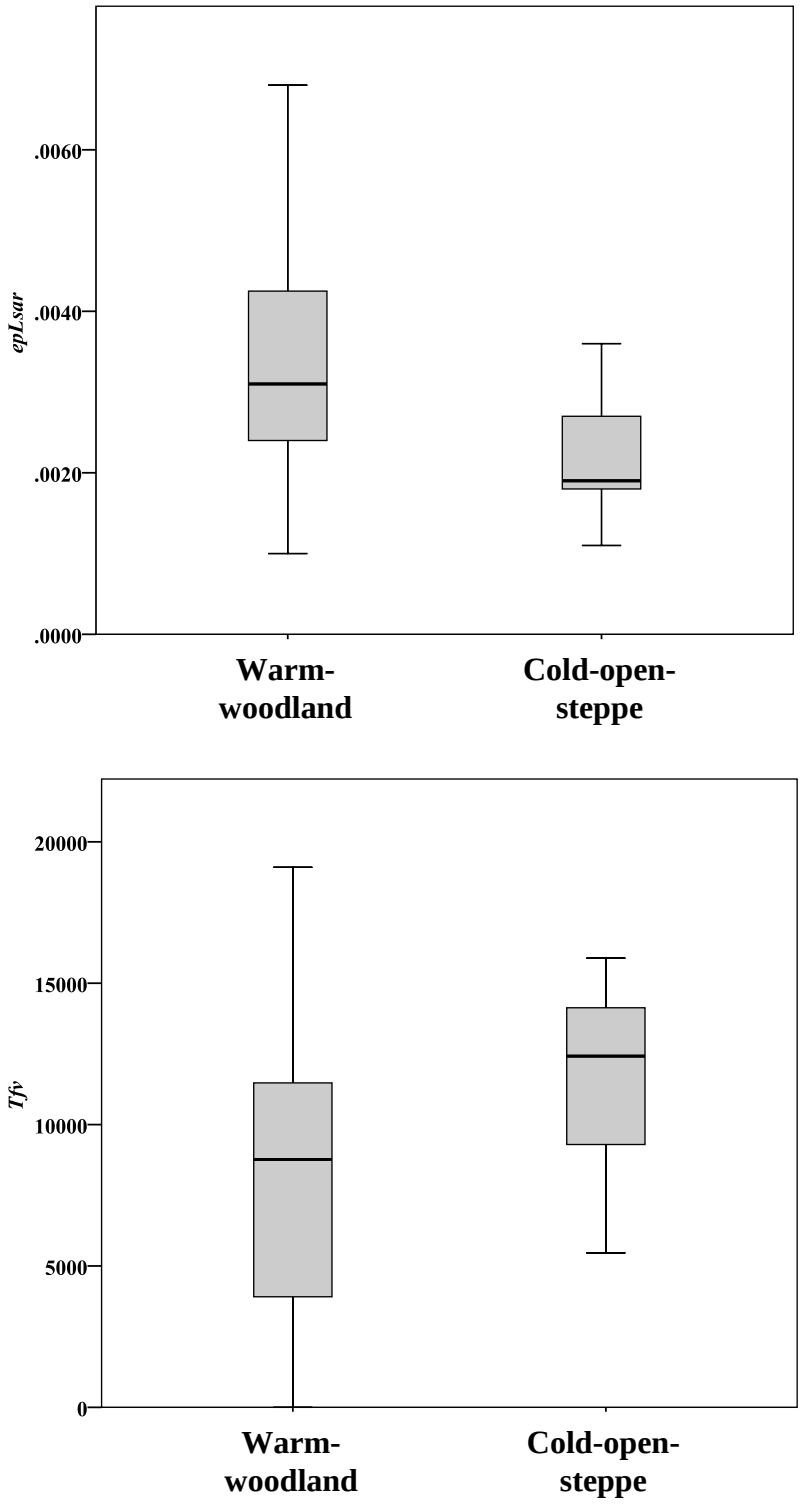


Figure 5.2: Box plots of Neandertal anisotropy (*epLsar*) and textural fill volume (*Tfv*) by climate.

Location

The descriptive statistics for the three locations, north, central, and south, are found in Table 5.7. The two-factor MANOVA also indicates that significant differences are found within three location subcategories, but Levene's test suggests that distribution variances remain homogeneous (Table 5.5). These location subgroups are based on latitude, with the northern category encompassing latitudes of 53° to 48°, the central group including 47° to 42°, and the southern latitudes comprising 41° to 32°.

The two-factor ANOVAs demonstrate that complexity (*Asfc*) and heterogeneity 9x9 ($HAsfc_{81}$) vary significantly by location (Table 5.8). This is interesting, as the texture variables shown to be significant in distinguishing Neandertals by climate are different from those that differentiate Neandertals by location. Additionally, since there are more than two subcategories in the location group, pairwise comparisons tests are necessary to determine the sources of significant variation.

Tukey's HSD pairwise comparisons indicate that the northern locations are significantly higher in complexity (*Asfc*) than both the central and southern groups. Moreover, pairwise comparisons tests indicate that the northern group has significantly higher heterogeneity 9x9 ($HAsfc_{81}$) than the southern group, and marginally higher[14] values than those of the central group. Additionally, the central group demonstrates marginally higher heterogeneity 9x9 ($HAsfc_{81}$) values than those of the southern group. Thus, there is a continuum of decreasing heterogeneity 9x9 values from northern to central to southern locations in Western Eurasia. See Table 5.9 for pairwise comparisons.

[14] As described in Chapter 3, Tukey's HSD test results are used as the benchmark for significance, though Fisher's LSD test results are considered suggestive, with $p < 0.05$ for this test but not the HSD test, implying marginal significance.

NEANDERTALS BY LOCATION: NORTH						
	Asfc	***Smc***	***epLsar***	***Tfv***	***HAsfc$_9$***	***HAsfc$_{81}$***
Mean	1.80	0.32	0.0026	12367.59	0.46	0.90
Median	1.81	0.27	0.0023	13156.18	0.46	0.96
SD	0.39	0.16	0.0013	2250.41	0.09	0.11
NEANDERTALS BY LOCATION: CENTRAL						
	Asfc	***Smc***	***epLsar***	***Tfv***	***HAsfc$_9$***	***HAsfc$_{81}$***
Mean	1.16	10.62	0.0029	9008.53	0.48	0.78
Median	1.00	0.42	0.0028	9582.77	0.47	0.73
SD	0.76	45.40	0.0012	4635.42	0.13	0.26
NEANDERTALS BY LOCATION: SOUTH						
	Asfc	***Smc***	***epLsar***	***Tfv***	***HAsfc$_9$***	***HAsfc$_{81}$***
Mean	0.90	7.79	0.0038	8011.84	0.43	0.61
Median	0.87	0.21	0.0039	8524.42	0.45	0.62
SD	0.46	24.74	0.0015	5823.29	0.10	0.12

Table 5.7: Descriptive statistics of the Neandertal sample by location. North *n* = 6, central *n* = 48, and south *n* = 11.

ANOVAs				
	Sum of Squares	***F***	**df**	***p***
Asfc	1977.10	3.07	2	0.05
epLsar	235.45	0.37	2	0.69
Smc	1097.76	1.55	2	0.22
Tfv	294.09	0.45	2	0.64
HAsfc9	473.43	0.70	2	0.50
HAsfc81	1993.65	3.43	2	0.04

Table 5.8: Location results from two-factor ANOVAs on ranked data.

MATRICES OF PAIRWISE DIFFERENCES		
Complexity (*Asfc*)		
	Central	Southern
Northern	**22.16**	**28.89**
Central		6.73
Heterogeneity 9x9 (*HAsfc $_{81}$*)		
	Central	Southern
Northern	15.20*	**28.23**
Central		13.03*

Table 5.9: Matrices of pairwise comparisons by location. Bolded numbers indicate Tukey's HSD and * denote Fisher's LSD (but not Tukey's HSD) significant results.

OIS number

The descriptive statistics for each texture variable by OIS number are found in Table 5.10. Levene's test does not show significant variation in the distribution variance of the texture attributes, while the overall MANOVA model indicates significant differences in texture attributes among the different OIS-based Neandertals. Individual ANOVAs indicate differences in three texture attributes: including textural fill volume, heterogeneity 3x3, and heterogeneity 9x9. See Table 5.11 for MANOVA and ANOVA results.

Tukey's HSD pairwise comparisons tests indicate the sources of significant variation within each texture variable. For textural fill volume, the OIS 6/5 subgroup shows significantly lower values than the other three groups. For heterogeneity 3x3 and 9x9, Tukey's HSD pairwise comparisons indicate that the OIS 4 Neandertals are significantly higher than those from OIS 6/5. Lastly, Fisher's LSD comparisons indicate that OIS 4 is also marginally higher in heterogeneity 9x9 than OIS 3. See Table 5.1

NEANDERTALS FROM OIS 3						
	Asfc	***Smc***	***epLsar***	***Tfv***	***HAsfc$_9$***	***HAsfc$_{81}$***
Mean	0.91	9.93	0.0035	11092.67	0.46	0.71
Median	0.87	0.74	0.0033	11041.15	0.49	0.75
SD	0.47	23.26	0.0018	3117.74	0.14	0.21
NEANDERTALS FROM OIS 4						
	Asfc	***Smc***	***epLsar***	***Tfv***	***HAsfc$_9$***	***HAsfc$_{81}$***
Mean	1.51	56.08	0.0025	13067.04	0.58	1.00
Median	1.29	0.54	0.0024	13277.91	0.57	0.98
SD	0.99	104.30	0.0009	2272.78	0.12	0.31
NEANDERTALS FROM OIS 5						
	Asfc	***Smc***	***epLsar***	***Tfv***	***HAsfc$_9$***	***HAsfc$_{81}$***
Mean	1.71	0.27	0.0027	11658.53	0.49	0.88
Median	1.38	0.27	0.0025	11203.73	0.45	0.74
SD	1.16	0.08	0.0014	4786.65	0.11	0.34
NEANDERTALS FROM OIS 6/5						
	Asfc	***Smc***	***epLsar***	***Tfv***	***HAsfc$_9$***	***HAsfc$_{81}$***
Mean	1.07	0.52	0.0029	6546.74	0.43	0.69
Median	1.01	0.42	0.0030	6047.77	0.42	0.67
SD	0.49	0.74	0.0011	4172.62	0.11	0.16

Table 5.10: Descriptive statistics of the Neandertal sample by OIS number. OIS 6/5 *n* = 28, OIS 5 *n* = 8, OIS 4 *n* = 8, and OIS 3 *n* = 13.

MANOVA					
		Test statistic	***F***	**df**	***p***
OIS	Pillai's Trace	0.59	2.06	18, 150	0.01
	Wilks' λ	0.49	2.16	18, 136.25	0.01
	Holtelling's Trace	0.87	2.25	18, 140	0.01
ANOVAs					
		Sum of Squares	***F***	**df**	***p***
	Asfc	1641.99	2.11	3	0.11
	epLsar	596.37	0.71	3	0.55
	Smc	1854.84	2.46	3	0.07
	Tfv	5458.09	9.67	3	0.00
	HAsfc9	2287.21	3.08	3	0.04
	HAsfc81	2112.24	2.80	3	0.05

Table 5.11: MANOVA and ANOVA results with OIS as a factor. Analyses performed on ranked data.

MATRICES OF PAIRWISE DIFFERENCES			
Textural Fill Volume (*Tfv*)			
	4	5	6/5
3	-8.61	-0.36	**16.34**
4		8.25	**24.95**
5			**16.70**
Heterogeneity 3x3 ($HAsfc_{9}$)			
	4	5	6/5
3	-12.95	-0.20	6.03
4		12.75	**18.97**
5			6.22
Heterogeneity 9x9 ($HAsfc_{81}$)			
	4	5	6/5
3	-14.60*	-6.29	2.84
4		8.31	**17.44**
5			9.13

Table 5.12: Matrices of pairwise comparisons by OIS number. Bolded numbers indicate Tukey's HSD and * denote Fisher's LSD (but not Tukey's HSD) significant results.

Discussion

These data provide substantial evidence for variation in Neandertal anterior dental microwear textures, and offer important clues regarding Neandertal subsistence and behavioral adaptations. While analyses of central tendencies offer information concerning differences in incisor microwear textures by climate, location, and OIS number, examinations of distribution variance can provide important details about the expanded or limited range of microwear textures. The interpretation for each independent variable, including climate, location, and OIS number, will be discussed separately.

Climate

The Neandertal sample, divided into two climate subcategories, warm-woodland and cold-open steppe, shows significant variation in anisotropy (*epLsar*) and textural fill volume (*Tfv*) for both measures of central tendencies and distribution variance. The scale of maximum complexity (*Smc*) also shows significant variation in variance, due largely to the outliers found in the cold-open-steppe Neandertal subcategory.

Bioarchaeological data presented in Chapter 4, coupled with previously published data (Krueger & Ungar, 2010) strongly support the anisotropy texture attribute as an accurate indicator of non-dietary anterior tooth use behaviors. Specifically, those bioarchaeological samples that are known or inferred to have used their anterior dentition in activities other than incising large food items present low anisotropy values. Conversely, those samples which are not documented to have engaged in these activities show higher anisotropy values.

This phenomenon can be attributed to the use of these teeth. It is predicted that if the anterior teeth are used to incise large food items, then those foods, or abrasives adherent to foods, will be dragged up the labial surface, creating apicocervically oriented striations. This would result in high anisotropy values. If, on the other hand, anterior teeth are used principally for non-dietary anterior tooth use behaviors, such as labret use, basketry activities, tool production or retouching, or clamping and grasping actions, then striations would be more limited on the labial surface.

The low mean anisotropy value (0.0022) for the cold-open-steppe Neandertals suggests these individuals were participating in non-dietary anterior tooth use behaviors. This value is most similar to that of the Ipiutak and Nunavut Territory samples, both of

which demonstrate an extremely low mean value of 0.0020. The Neandertal value is also just lower than that of the Prince Rupert Harbour sample value of 0.0024. All three of these bioarchaeological samples participated in non-dietary anterior tooth use behaviors, but in different ways. While the Ipiutak and Nunavut Territory samples are hypothesized to have used their anterior dentition in intense processing of caribou hide for personal clothing as well as for trade, the Prince Rupert Harbour sample used their anterior teeth in basketry production and labret use.

The mean anisotropy value (0.0033) for the warm-woodland Neandertals is in between non-dietary anterior tooth use and dietary use of the anterior teeth. The nearest bioarchaeological comparative samples are that of the Tigara, with a mean value of 0.0032 and the Fuegian and Amarna samples, both with mean values of 0.0034. While the Tigara are recorded as using their anterior dentition as a tool, it was not to the degree as some of the other arctic samples. On the other hand, neither the Fuegian nor Amarna samples are known to have employed these behaviors. Consequently, a conservative interpretation suggests that the warm-woodland Neandertals may have utilized non-dietary anterior tooth use behaviors, but certainly not to the degree or frequency of the cold, steppe Neandertals.

The significant difference in variance between these two subcategories may provide additional information about the range of their adaptive strategies. The limited range of variation in the cold-open-steppe Neandertals may indicate the narrow range of anterior tooth use behaviors available to these individuals. Interestingly, the range of anterior tooth use behaviors in the cold-open-steppe Neandertals lies nearly entirely within the range of the comparative groups that engaged in non-dietary anterior tooth use.

On the other hand, the expanded range of values of the warm-woodland Neandertals may suggest these individuals had more variability in their anterior tooth use behaviors. Indeed, their range of values lies within both the non-dietary and dietary anterior tooth use values.

Therefore, the cold-open-steppe Neandertals possess both a very low mean anisotropy value and a constricted range of values, nearly all of which are within the range of the comparative groups that engaged in non-dietary anterior tooth use. This suggests these individuals were restricted in their anterior tooth behaviors, and chose to focus them on non-dietary forms of tooth use. On the other hand, the warm-woodland Neandertals have a higher mean anisotropy value, in addition to a wide range of variance. This indicates that these Neandertals had a wider range of anterior tooth use behaviors available to them. While they sometimes may have utilized non-dietary forms, they also employed dietary types of tooth use.

The fact that these differences are found among climates suggests that this factor played a role in not only amount of non-dietary anterior tooth use, but also in the type of behaviors utilized by these different Neandertal groups. That is, while the cold-open-steppe Neandertals focused their anterior tooth use on non-dietary activities, perhaps due to hide preparation for protection from the harsh, open environments, the warm-woodland Neandertals did not have to concentrate on these activities. Perhaps the warm-woodland Neandertals benefited from their environment given that they did not have to pursue non-dietary anterior tooth use behaviors as intensely as the cold-open-steppe Neandertals, and, in addition, could exploit a wider breadth of both animal and plant resources that accompany a warmer environment. Indeed, evidence for a broad resource

base with both plant and marine exploitation is found in the paleoanthropological record, including sites in the Levant (Madella et al., 2002), France (Anderson-Gerfaud, 1990; Hardy, 2004), Italy (Stiner, 1994), Portugal (Antunes, 2000a,c; Antunes et al., 2000), Spain (Vaquero et al. 2001), Gibraltar (Stringer et al., 2008), and various sites in Europe (Patou-Mathis, 2004; Henry et al., 2010).

These two subcategories also demonstrate significant differences in textural fill volume (*Tfv*) means and variance. Textural fill volume has been useful in bioarchaeological analyses for determining high magnitude or repetitive loading of the anterior teeth or abrasive particle density or size (Krueger & Ungar, 2010). Specifically, this texture attribute provides a more complete representation of possible activities or adaptations. Textural fill volume values that accompany low anisotropy in bioarchaeological samples have provided indications of specific tasks in relation to non-dietary anterior tooth use behaviors. Conversely, textural fill volumes that accompany high anisotropy values in bioarchaeological groups have signaled abrasive particle density or size.

For example, the Nunavut Territory and Ipiutak samples have the lowest average anisotropy values of all the modern human comparative samples, with a mean value for both groups of 0.0020. Additionally, they have the highest textural fill volume values (12,449 and 12,143, respectively). The combination of low anisotropy and high textural fill volume is interpreted as a similarly intense non-dietary anterior tooth use regimen that required high magnitude and/or repetitive loading of the anterior teeth. This is hypothesized to be concentrated preparation and utilization of caribou hide and sinew for clothing and boot production by these individuals.

Likewise, the cold-open steppe Neandertals demonstrate extremely high textural fill volume values. Indeed, they are significantly higher than those of the warm-woodland Neandertals, with a mean value of 11,719. The combination of the low anisotropy (0.0022) and the high textural fill volume (11,719), is very similar to the values of the Ipiutak and Nunavut Territory samples. This suggests the cold-open-steppe Neandertals may have used their anterior dentition in much the same way as these modern human samples. Perhaps these Neandertals focused on non-dietary anterior tooth use behaviors associated with incisal grasping or clamping, such as in intense hide or sinew production. The cold-open-steppe climate conditions would have required some form of protective covering, and perhaps these individuals were preparing hides for sustained or prolonged protection from the environment.

Indeed, evidence for the necessity of protective coverings is found in inferences of Neandertal critical and minimum sustainable temperatures, in which even insulation resulting from their increased muscle mass and dietary-related elevated basal metabolic rate (BMR) would not have been sufficient in tolerating or surviving the cold-open conditions (Aiello & Wheeler, 2003). Additionally, archaeological evidence for these behaviors are found in lithic and faunal assemblages at several sites, including Corbiac, Pech de l'Aze, and Combe Grenal, where lithic microwear analyses suggested nearly 10% of the retouched tools displayed evidence for hide preparation (Anderson-Gerfaud, 1990). Similar lithic microwear analyses at La Quina also found evidence for hide preparation (Hardy, 2004), and sites from southeastern France and northwestern Italy demonstrate cut marks on cave bear bones indicative of opportunistic acquisition of fur resources (Valensi & Psathi, 2004).

Several cold-open-steppe sites also show a pattern indicative of reindeer intercept hunting (Oakley et al., 1971; Mellars, 1996; Rink et al., 1996; Gaudzinski, 2000; Gaudzinski & Roebroeks, 2000; Costamagno et al., 2006). Perhaps this resource was selected not only for its meat and marrow food resources, but also for its hide and sinew to produce protective coverings (Gaudzinski, 2000; Gaudzinski & Roebroeks, 2000). Interestingly, a faunal assemblage analysis of the northern German site of Salzgitter Lebenstedt found the remains of 86 reindeer individuals, with the majority taken during autumn (Gaudzinski, 2000; Gaudzinski & Roebroeks, 2000). One might speculate that this assemblage could represent the preferential hunting of reindeer for not only meat and marrow purposes, but also for hide resources to prepare for the approaching winter.

The warm-woodland Neandertals, on the other hand, demonstrate lower textural fill volume values than those of the cold-open steppe group, with a mean value of 8,240. The textural fill volume values, just as with the anisotropy values of this subgroup, straddle the line between two different interpretations, either high magnitude or repetitive loading of the anterior teeth, or abrasive particle density and size. Specifically, the two modern human comparative samples that are nearest this value are the Tigara (7,296) and the Fuegian (9,151).

While the Tigara sample has an anisotropy mean value of 0.0032 and a textural fill volume mean of 7,296, the Fuegian sample has an anisotropy mean value of 0.0034 and a textural fill volume mean of 9,151. The Tigara sample is recorded as participating in non-dietary anterior tooth use behaviors specifically related to hide preparation, but not as intensely or using the same animal hide resources as that of the Ipiutak and Nunavut Territory samples (Birch, 1981; Foote, 1992). On the other hand, the Fuegian sample did

not use their anterior dentition as a tool, and were exposed to high abrasive loads related to a diet primarily of marine resources, as well as heavy winds along these subsistence areas (Yesner et al., 2003). Their high anisotropy and textural fill volume values are congruent with this ethnographic information.

As described above, the warm-woodland Neandertal sample has an anisotropy mean value of 0.0033 and a textural fill volume value of 8239.98. These intermediate values between non-dietary anterior tooth use with high magnitude and/or repetitive loading and dietary anterior tooth use with high abrasive exposures suggest that these Neandertals employed a wide range of anterior tooth use activities. Perhaps during colder periods, these Neandertals were able to use their anterior dentition as a tool for the production of protective coverings. The absence of reindeer in these areas also favors the exploitation of other herbivores, perhaps red deer or roe deer. However, it seems as though the warm-woodland Neandertals were also able to exploit a wider range of plant and marine resources, and exposure to a variety of abrasive particle sizes and types may explain the high textural fill volume values.

Providing support for this interpretation is the distribution variance for the textural fill volume values. As with anisotropy, there is a significant difference between the cold-open-steppe Neandertals and the warm-woodland sample. Specifically, the cold-open-steppe Neandertals demonstrate a constricted variance, while the warm-woodland sample shows a greatly expanded range of values. This is important, as it reinforces the idea put forth for the same pattern found for the anisotropy variance, in which the constriction of the cold-open-steppe sample appears to signify a limitation to anterior tooth use behaviors. As posited above, perhaps the emphasis for this sample needed to be

on the production of protective coverings for the cold, harsh environment. On the other hand, the expanded range of variance for the warm-woodland Neandertal sample suggests a much greater diversity in anterior tooth use behaviors, with these individuals not only able to employ non-dietary, but also dietary anterior tooth use activities.

Location

When the Neandertal sample is divided into three location subcategories, north, central, and south, it demonstrates significant differences in central tendencies in heterogeneity 9x9 ($HAsfc_{81}$) and complexity ($Asfc$). There are no significant differences in distribution variance for any texture variable by location. First, an interpretation of the heterogeneity 9x9 texture attribute is discussed, and then one for complexity follows.

Heterogeneity 9x9, the fine-scale variant of the heterogeneity attribute, was not shown to be important in distinguishing incisor microwear textures in previous bioarchaeological analyses (Krueger & Ungar, 2010). However, significant differences were found when eight other bioarchaeological samples were added to the analyses. Although preliminary and requiring additional testing, this texture attribute is suggested to be indicative of dietary and environmental abrasive loads; however, the practice of non-dietary anterior tooth use behaviors exacerbates the signal.

Many of the bioarchaeological samples are coastal, but do not display the same high heterogeneity 9x9 values as some of the others. Namely, those from the coastal arctic areas demonstrate extremely high heterogeneity 9x9 values, and not only were exposed to high abrasive loads, but also participated in non-dietary anterior tooth use

activities. Therefore, it was suggested in Chapter 4 that non-dietary anterior tooth use behaviors play a role in the high variation of microwear textures.

Tukey's HSD and Fisher's LSD pairwise comparisons show that the northern Neandertal group has significantly higher heterogeneity 9x9 than does the southern group, and marginally higher values than those of the central group. This is indicative of a decrease in heterogeneity 9x9 values from north to central to south. If the revised hypothesis from Chapter 4 is correct, this suggests that the northern Neandertals were exposed to higher amounts of dietary and/or environmental abrasives than the other two subcategories. However, the low anisotropy values of the northern Neandertals support non-dietary anterior tooth use behaviors, which may be intensifying the heterogeneity signal of this subgroup.

Moreover, the central group demonstrates marginally higher $HAsfc_{81}$ values than those of the southern group. This suggests that the centrally located Neandertals were exposed to more dietary and/or environmental abrasives than those in the southern area, but less than those in the North. The low anisotropy value, although not as low as that of the northern Neandertals, also suggests that moderate non-dietary anterior tooth use may be exacerbating the central Neandertal heterogeneity 9x9 values.

If the revised hypothesis from Chapter 4 is correct, then the low heterogeneity values of the southern Neandertals suggest that these individuals were exposed to a low variety of abrasive sizes or types. The high anisotropy value for this subgroup indicates dietary use of the anterior dentition only. Therefore, in line with the revised hypothesis, the heterogeneity value can be attributed to abrasive loads only.

Although complexity is important in molar microwear texture studies, this attribute was not shown to be useful in distinguishing incisor microwear textures in a previous study (Krueger & Ungar, 2010). However, when additional bioarchaeological samples were added, this texture variable showed significant variation. This result was tentatively interpreted in Chapter 4 as the product of two factors: 1. the level of exposure to different sizes and/or types of abrasives and 2. the level of non-dietary anterior tooth use behaviors.

If a sample was exposed to high abrasive loads, as indicated by high heterogeneity, and participated in non-dietary anterior tooth use, as indicated by low anisotropy, their complexity values may be exceedingly high. This is suggested for the Ipiutak and Nunavut Territory samples, both of which have high heterogeneity averages, low anisotropy values, and high complexity values as well.

If the sample was exposed to only high abrasive loads *or* individuals participated in non-dietary anterior tooth use activities, moderate complexity is predicted to be present. Indeed, the Illinois Bluff and Puye samples have moderate complexity values, which possibly results from the former's non-dietary anterior tooth use behaviors and low abrasive loads and the latter's high abrasive loads but dietary use of the anterior dentition. Lastly, those samples with abrasive loads and a lack of non-dietary anterior tooth use should result in low surface roughness, or complexity.

The northern Neandertal sample demonstrates significantly higher complexity values than both the central and southern Neandertal groups. This is not surprising considering their high mean value of 1.80. The most similar bioarchaeological sample is that from Prince Rupert Harbour, with a mean complexity value of 1.85. This modern

human sample's high value is not as high as those from Ipiutak and Nunavut Territory; however, it still is significantly higher than all other samples. Their high complexity values are unsurprising as these three arctic samples all utilized non-dietary anterior tooth use behaviors and were exposed to high abrasive loads. Similarly, the northern Neandertal sample has low anisotropy values, suggesting non-dietary anterior tooth use behaviors, high heterogeneity values, indicative of high abrasive loads exacerbated by non-dietary behaviors, and, consequently, high complexity values.

It is interesting to note the continuum of texture attribute values among the northern, central, and southern Neandertal subcategories. That is, there is a steady increase in anisotropy from northern to central to southern Neandertals. This suggests a decrease in non-dietary anterior tooth use behaviors in relation to latitude, and is most likely related to climate. On the other hand, the heterogeneity 9x9 values decrease from north to central to southern Neandertal populations. This suggests a decrease in abrasive exposure by latitude. Thus, there is a pattern from north to central to south of increasing anisotropy values and decreasing heterogeneity 9x9 values. If the hypothesis holds true that non-dietary anterior tooth use behaviors and abrasive loads affect the complexity variable, one would expect a decrease in complexity from north to central to south. And this is exactly what happens.

OIS number

The Neandertal sample, divided into OIS 6/5, 5, 4, and 3, has significant variation in textural fill volume, heterogeneity 3x3, and 9x9. Tukey's HSD pairwise comparisons tests indicate that for textural fill volume, the OIS 6/5 subcategory has significantly lower

values than the other three OIS samples. Indeed, this subcategory is considerably lower than the others, with a mean value of 6547. Textural fill volume, as described above, has been related to either high magnitude and/or repetitive loading of the anterior teeth in non-dietary anterior tooth use activities or tentatively as a proxy for abrasive particle density or size.

The moderately low anisotropy mean value of 0.0029 suggests that the OIS 6/5 Neandertals did participate in non-dietary anterior tooth use, but not as often as interpreted for the cold-open-steppe Neandertals (it is interesting to note that the Neandertal sample from OIS 4, a cold, stadial interval, demonstrates the lowest mean anisotropy value and most constricted anisotropy variance of all the OIS subcategories). Consequently, the moderate textural fill volume values were most likely produced from these activities.

The Prince Rupert Harbour bioarchaeological sample also demonstrates low anisotropy (0.0024), and moderate textural fill volume values (5767). This signal was suggested to be from non-dietary anterior tooth use behaviors related to labret use and basketry production. Specifically, fibers were softened with the anterior dentition prior to weaving practices. Perhaps the OIS 6/5 Neandertals were participating in regimens that required similar behavioral adaptations. At the very least, they were not utilizing their anterior teeth in intense grasping or clamping activities as documented for the Ipiutak and Nunavut Territory, and proposed for the cold-open-steppe Neandertals.

Tukey's HSD pairwise comparisons indicate that the OIS 4 values are significantly higher in heterogeneity 3x3 and 9x9 than those for OIS 6/5. Moreover, Fisher's LSD comparisons show that OIS 4 is marginally higher in heterogeneity 9x9 than

is OIS 3. Indeed, the 3x3 and 9x9 mean values for the OIS 4 subcategory are 0.58 and 1.00, respectively.

Heterogeneity 3x3 and 9x9, as discussed in Chapter 4 and above, is interpreted as a proxy for abrasive exposure, but this attribute is exacerbated by non-dietary anterior tooth use behaviors. That is, samples will exhibit high heterogeneity values when they are exposed to high abrasive loads, but this signal will be exacerbated if the sample participates in non-dietary anterior tooth use. If only dietary anterior tooth use is recorded, then the heterogeneity variable is suggested to be due to abrasive loads alone.

The significantly and marginally higher heterogeneity 3x3 and 9x9 values of the OIS 4 Neandertals suggest these individuals were exposed to high dietary and/or environmental abrasive loads. However, the low anisotropy mean of 0.0025 for the OIS 4 Neandertals indicates non-dietary anterior tooth use, and these practices could be intensifying the heterogeneity signal. Indeed, the closest bioarchaeological sample is the Nunavut Territory, with mean 3x3 and 9x9 values of 0.60 and 1.09. This sample is coastal, reported to have been exposed to high abrasive loads, and hypothesized to use their anterior dentition in intense and focused caribou hide preparation. Therefore, it is parsimonious to propose that the high heterogeneity 3x3 and 9x9 values for the OIS 4 Neandertals are due to a combination effect of high abrasive loads and non-dietary anterior tooth use.

OIS 3 Neandertals

Oxygen isotope stage 3 is recognized as an interval of rapid oscillations of global climate that brought with it megafaunal extinctions not only in Europe, but the world.

Some have considered the Neandertals to be just another megafaunal victim of these oscillations (Stewart et al., 2003), while others have suggested that competition with anatomically modern humans was the source of their demise (Stringer & Gamble, 1993; Skinner, 1997; Gat, 1999; Mellars, 1999; Richards et al., 2001; Svoboda, 2005). Other studies have combined climate and competition, with these two factors comprising different percentages of the culpability (Stringer & Grün, 1991; Bocquet-Appel & Demars, 2000). A closer examination of the anterior dental microwear signatures of the OIS 3 Neandertals is warranted in the wake of these ideas, and perhaps inferences of dietary and behavioral strategies of these lingering Neandertals can help inform us on the probable cause(s) of the extinction of this, the last of the fossil hominin species.

Anisotropy is likely the most important variable in anterior dental microwear texture analyses. The high mean value of the OIS Neandertals, 0.0035, suggests that these individuals were not engaging in non-dietary anterior tooth use behaviors. This is a deviation from the other OIS intervals, which demonstrate a fairly constant anisotropy signal, situated within the range of non-dietary anterior tooth use activities.

Textural fill volume has been considered a proxy for differentiating forms of non-dietary anterior tooth use behaviors. For groups in which these behaviors have not been documented, *Tfv* is used as an indicator of abrasive particle density. The high anisotropy values of the OIS 3 Neandertals suggest the *Tfv* values are an indicator of the latter, rather than the former. Therefore, the extremely high textural fill volume mean value of 11,093 suggests these Neandertals were exposed to high abrasive densities.

The heterogeneity 3x3 and 9x9 values confirm the textural fill volume signal. The heterogeneity variable serves to approximate the level of exposure to dietary and/or

environmental abrasives, but is exacerbated by non-dietary anterior tooth use. The mean 3x3 and 9x9 values of the OIS 3 Neandertals are 0.46 and 0.71, both of which are moderately high values, but not exceedingly high as found in bioarchaeological samples exposed to high abrasive loads and reported to engage in non-dietary anterior tooth use behaviors. Lastly, the complexity value, positively correlated to heterogeneity in Chapter 4, is the lowest of all the OIS intervals, and indicates the small change in roughness over the scales of observation.

The texture attributes facilitate a more complete picture of the anterior dental microwear signatures of these Neandertals, and also allow assessment of variation through time. It is interesting that the overall OIS 3 Neandertal signal suggests that they were not engaging in non-dietary anterior tooth use; this marks a considerable behavioral divergence from the pattern formed from the previous OIS Neandertals. However, unlike the other OIS intervals, the OIS 3 sample is comprised of individuals from both cold-open-steppe sites (Kůlna, Le Moustier, Le Petit-Puymoyen, Marillac, and Saint-Césaire) and warm-woodland/semi-arid sites (Amud, Vindija, and Zafarraya). The descriptive statistics for the OIS 3 Neandertals by climate are presented in Table 5.13.

NEANDERTALS FROM OIS 3						
	Asfc	***Smc***	***epLsar***	***Tfv***	***HAsfc$_9$***	***HAsfc$_{81}$***
Mean	0.91	9.93	0.0035	11092.67	0.46	0.71
Median	0.87	0.74	0.0033	11041.15	0.49	0.75
SD	0.47	23.26	0.0018	3117.74	0.14	0.21
NEANDERTALS FROM OIS 3: WARM-WOODLAND						
	Asfc	***Smc***	***epLsar***	***Tfv***	***HAsfc$_9$***	***HAsfc$_{81}$***
Mean	0.83	15.82	0.0045	11520.20	0.47	0.64
Median	0.61	3.01	0.0047	11194.59	0.50	0.66
SD	0.47	28.70	0.0015	3044.26	0.14	0.15
NEANDERTALS FROM OIS 3: COLD-OPEN-STEPPE						
	Asfc	***Smc***	***epLsar***	***Tfv***	***HAsfc$_9$***	***HAsfc$_{81}$***
Mean	1.05	0.49	0.0020	10408.62	0.45	0.82
Median	1.05	0.42	0.0018	10890.88	0.47	0.85
SD	0.49	0.38	0.0008	3463.01	0.16	0.25

Table 5.13: Descriptive statistics for the OIS 3 Neandertals. Top data are for the OIS 3 Neandertals as a whole (*n* = 13), center data are for the warm-woodland individuals (*n* = 8), and bottom data (*n* = 5) are for the cold-open-steppe Neandertals.

Although the sample sizes for each climate division are small, results are suggestive. The anisotropy mean value for the cold-open-steppe Neandertals is extremely low, whereas the value for the warm-woodland sample is extremely high. While the cold-open-steppe Neandertals of OIS 3 continued non-dietary anterior tooth use activities, those of the warm-woodland OIS sites evidently did not. It is retrodicted that the high anisotropy value of the latter subsample signals a wider breadth of dietary resources, whereas the low value for the former subsample indicates an intense regimen of non-dietary anterior tooth use. This divergence indicates differences in adaptive strategies during the same chaotic timeframe, but different climate conditions.

The textural fill volume mean values are similar, with the cold-open-steppe Neandertals displaying a negligibly smaller mean value. The low anisotropy, coupled

with the high textural fill volume, possibly signals clamping or grasping with the anterior dentition in the cold-open-steppe subsample, perhaps related to the preparation of hides for protective coverings. On the other hand, the high anisotropy and *Tfv* values of the warm-woodland subsample suggest high exposure to abrasives.

The heterogeneity 9x9 also hints at these differences, as the cold-open-steppe subgroup has a considerably higher $HAsfc_{81}$ mean value. This reinforces the notion that heterogeneity, which signals levels of abrasive exposure, is exacerbated by non-dietary anterior tooth use behaviors. Therefore, the heterogeneity 9x9 signal of the warm-woodland OIS 3 Neandertals indicates abrasive exposure alone. This idea is supported by the complexity values, linked to heterogeneity, which shows the cold-open-steppe Neandertals with a higher mean value than that of the warm-woodland subsample.

Can we gain hints about the demise of the Neandertals through differences in anterior dental microwear signatures? The differences in anisotropy between the two OIS 3 subsamples suggest differences in Neandertal behavior during the turbulent climate oscillations. While the warm-woodland Neandertals evidently used their anterior dentition in dietary activities, perhaps benefiting from a wider breadth of plant and/or marine resources found in warmer areas, the cold-open-steppe Neandertals likely did not. In fact, their extremely low anisotropy values suggest the cold-open-steppe individuals were intensely using their anterior teeth in clamping and grasping activities, perhaps related to hide preparation for protective coverings.

If the cold-open-steppe Neandertals of OIS 3 were reliant on animal hide to live in the harsh environment, more and more animal hides would have been required as the climate continued to deteriorate toward the last glacial maximum (LGM). During this

time, several types of European megafauna became extinct, including the straight-tusked elephant (*Elephas antiquus*) and the Merck's rhinoceros (*Stephanorhinus kirchbergensis*) (Stewart et al., 2003). Moreover, species commonly associated with Neandertals, including reindeer (*Raingifer tarandus*), elk (*Alces alces*), chamois (*Rupicapra rupicapra*), ibex (*Capra ibex*), and musk ox (*Ovibos moschatus*) migrated north and/or to higher elevations (Stewart et al., 2003). Perhaps the extinction and/or migration of key dietary and hide resources, initiated by the deteriorating climate conditions of OIS 3, led to the extinction of the cold-open-steppe Neandertals. Under this premise, it is unsurprising that the last area of Neandertal existence is documented on the Iberian Peninsula (Zilhão, 1996; Finlayson et al., 2006).

Conclusion

Neandertal anterior dental microwear texture signals vary between climate types, location areas, and OIS number. Specifically, the two climate types, cold-open-steppe and warm-woodland, differed significantly in anisotropy and textural fill volume central tendencies and distribution variance. The anisotropy variable has been useful in bioarchaeological analyses in determining the application of non-dietary anterior tooth use regimens within a population (Krueger & Ungar, 2010). Specifically, low anisotropy is suggested to correlate with non-dietary anterior tooth use, while high anisotropy is linked with dietary purposes (Krueger & Ungar, 2010). The cold-open-steppe Neandertals demonstrated significantly lower anisotropy values than those of the warm-woodland sample. This suggests the cold-steppe Neandertals used their anterior dentition in non-dietary anterior tooth use behaviors more intensely than the warm-woodland Neandertals.

We gain even more insights when results for anisotropy are interpreted in light of textural fill volume. Textural fill volume is supported in Krueger & Ungar (2010) and Chapter 4 to be a useful indicator of high magnitude and/or repetitive loading of the anterior dentition or tentatively as a proxy for abrasive particle density and size. The key element in its differentiation is the anisotropy value. If anisotropy is low, the *Tfv* value can be used to suggest specific tasks associated with non-dietary anterior tooth use behaviors. If anisotropy is high, the *Tfv* values can be tentatively associated with abrasive particle density and size. With this in mind, the significantly higher *Tfv* value of the cold, steppe Neandertals coupled with their extremely low *epLsar* values suggests intense non-dietary tooth use practices. In fact, the cold-open-steppe Neandertal sample values are nearly identical to those of the Ipiutak and Nunavut Territory bioarchaeological samples, two arctic groups which practiced intense and concentrated caribou hide production for clothing, boots, and trade purposes. It is suggested that perhaps the cold-open-steppe Neandertals were performing similar activities for survival in the harsh environment.

The warm-woodland Neandertals showed moderately high *Tfv* values and moderately low *epLsar* values. Their signal was most similar to that of the Tigara, a high arctic, whale hunting sample from Point Hope, Alaska. Although these individuals used their anterior dentition in hide production, caribou was not frequently or readily available in the area, so they used other types of animals, such as seal or walrus, in its place (Foote, 1992). As described in Chapter 4, the hides from these sea mammals were lightly processed to maintain stiffness, and internal organs, such as bladders, stomachs, and intestine, did not require much, if any, anterior tooth use for preparation (Foote, 1992).

The signal of the warm-woodland sample, therefore, suggests similar anterior tooth use activities to that of the Tigara sample; specifically, clamping and grasping activities that were not as intense or frequent as the cold-open-steppe subsample.

The distribution variance of these two texture variables also shows significant variation, with the cold-open-steppe Neandertals having constricted anisotropy and textural fill volume values. This suggests that the cold-open-steppe Neandertals were focused on non-dietary anterior tooth use behaviors, most likely in the form of protective covering production, while the warm-woodland Neandertals participated in a range of tooth use activities, including both non-dietary and dietary components. This is suggested to reflect their expanded dietary breadth, such as plant and marine resources, as well as a less use of the front teeth to manufacture protective coverings than would be expected in colder climates.

Neandertals also differ in anterior textures in relation to their location. Specifically, the northern subsample show significantly and marginally higher heterogeneity 9x9 values than the southern and central groups, respectively. Moreover, the central group has marginally higher values than those from the south. Heterogeneity has been interpreted as an indicator of dietary and/or environmental abrasive loads; however, non-dietary anterior tooth use exacerbates the signal. Although it is likely that the abrasive load exposure decreased from north to central to south, the low anisotropy values for the northern and central subsamples most likely exacerbates the signal.

Complexity also differed by location, and is positively correlated to heterogeneity. That is, surface roughness is positively correlated to surface variation. This is tentatively suggested to be due to the combined or singular effects of non-dietary anterior tooth use

behaviors and/or abrasive loads. The northern Neandertals show significantly higher complexity values than the central or southern Neandertals. In line with the provisional hypothesis, this may related to the combined effect of high abrasive loads, as indicated by heterogeneity, and non-dietary anterior tooth use, as suggested by the low anisotropy value.

Lastly, the Neandertal sample varies significantly in microwear texture attributes by OIS number. The OIS 6/5 Neandertals have significantly lower *Tfv* values than all other OIS intervals, including OIS 5, 4, and 3. The low anisotropy values indicates this likely reflects fill volume due to non-dietary anterior tooth use. The OIS 6/5 Neandertal values were most similar to those of Prince Rupert Harbour, a sample of Canadian Inuit that used their anterior dentition in softening basketry fibers. Although it is radical to suggest Neandertals were producing baskets, perhaps the OIS 6/5 Neandertals simply used their anterior dentition in activities with a similar loading regimen.

For heterogeneity 3x3 and 9x9, the OIS 4 Neandertals are significantly higher than OIS 6/5, and also marginally higher in heterogeneity 9x9 than OIS 3. Heterogeneity values, as detailed above, likely reflect abrasive load, but non-dietary anterior tooth use exacerbates the signal. Thus, it is suggested that the higher value of OIS 4 is related to not only their abrasive loads, but also their non-dietary tooth use practices.

Lastly, the OIS 3 Neandertals require further consideration, since this turbulent climatic time period is the interval in which this, and other megafauna of Europe, became extinct. The overall OIS 3 Neandertal signal indicates a divergence from the other OIS Neandertals in their practice of non-dietary anterior tooth use behaviors. Namely, these

individuals have a high mean anisotropy value, suggesting only dietary use of the anterior teeth.

However, when the OIS 3 Neandertals were separated by climate conditions, the cold-open-steppe Neandertals of OIS 3 have lower anisotropy and higher *Tfv*. This suggests that these cold-climate individuals were using their anterior dentition intensely in clamping or grasping activities, most likely related to the production of protective coverings. The warm-woodland Neandertals have higher anisotropy and textural fill volume values, suggesting only dietary tooth use practices coupled with high abrasive loads.

It is proposed that the anterior dental microwear patterns of cold-open-steppe Neandertals of OIS 3 reflect an intense regimen of hide preparation for the production of protective coverings. As the climate continued to deteriorate into the last glacial maximum, an increased demand for such protective coverings would have occurred; however, megafauna went extinct, as other Neandertal-associated fauna migrated north or into mountainous areas, limiting or even eliminating contact with these individuals (Stewart et al., 2003). Perhaps these Neandertals were not able to adapt to these changing, and increasingly inhospitable conditions, and only those left remaining in the warmer, more tempered climates were able to remain (Zilhão, 1996; Finlayson, 1999; 2006).

CHAPTER SIX: ANATOMICALLY MODERN HUMANS

Results

Forty-two adult anatomically modern humans (AMH) examined for this study preserved microwear texture signatures. These individuals date from OIS 3 to OIS 2, and are situated in the Levant and throughout Europe. The most northern and eastern individuals used in this study are those from Dolní Věstonice and Pavlov in the Czech Republic, the most southern are those from several sites in Israel, and the most western are from several clustered sites in southwestern France (Fig. 6.1). The descriptive statistics for the entire AMH sample are presented in Table 6.1.

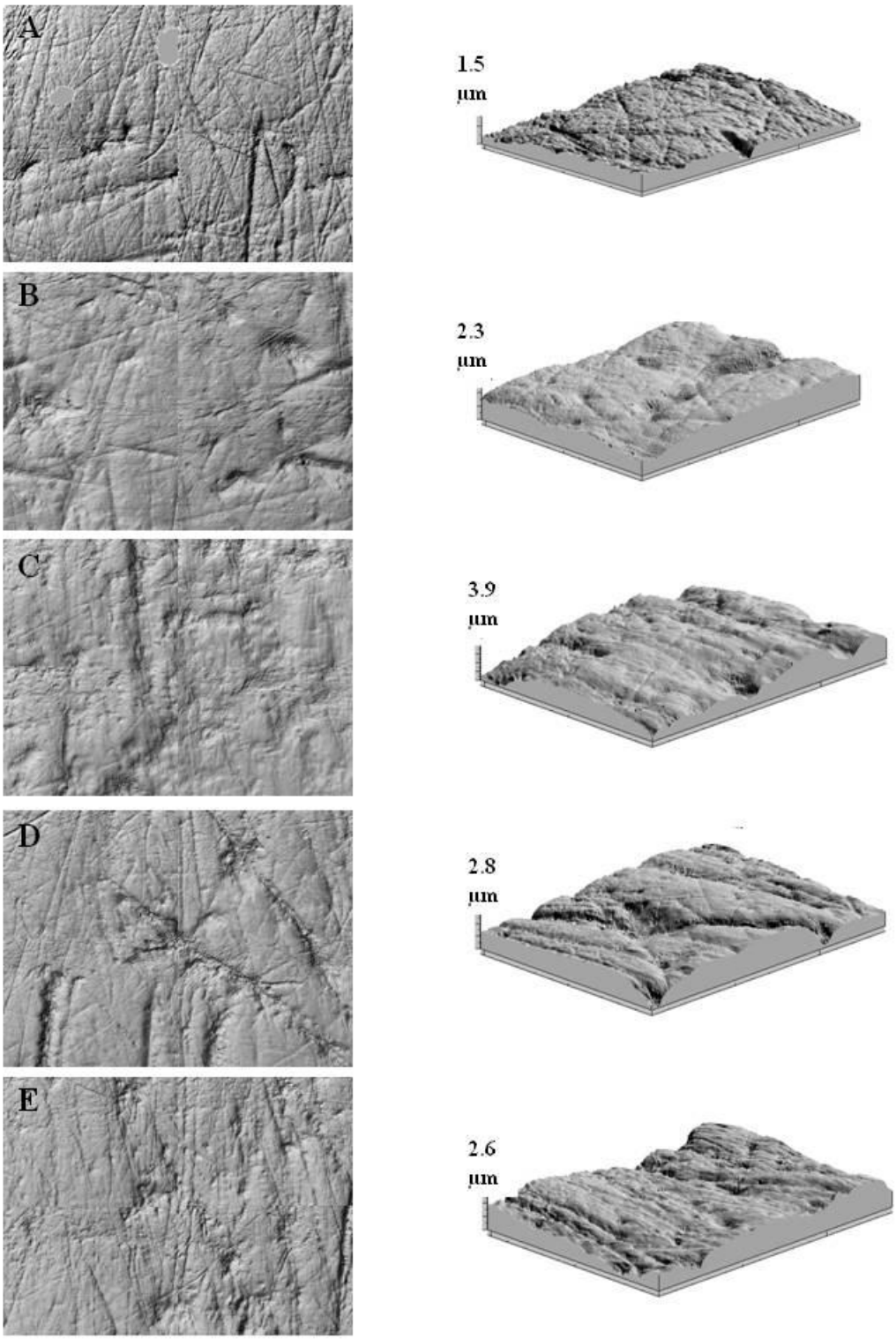
AMH OVERALL						
	Asfc	***Smc***	***epLsar***	***Tfv***	***HAsfc9***	***HAsfc81***
Mean	1.29	1.39	0.0033	9562.30	0.55	0.86
Median	1.07	0.27	0.0032	11631.48	0.44	0.73
SD	0.81	4.27	0.0012	5583.85	0.35	0.39

Table 6.1: Descriptive statistics of the entire AMH sample, *n* = 42.

As with the Neandertal sample, upper and lower central and lateral incisors and canines are used in the analysis of the AMH, and a two-factor MANOVA was performed to ensure no differences existed in microwear textures by tooth type or jaw. Canines were excluded from this statistical test because the sample size by jaw violated the MANOVA assumption of the sample size being greater than or equal to the number of dependent variables (three mandibular canines and two maxillary canines). Consequently, a two-factor MANOVA was completed on ranked microwear texture data in which tooth type (central and lateral incisors) and jaw (maxilla and mandible) were listed as the factors, and the microwear texture attributes were the dependent variables.

This statistical test shows no significant interaction between tooth type and jaw, or significant differences in microwear textures in tooth type or jaw (Table 6.2). This

suggests, as with the Neandertal data, that regardless of the tooth type or jaw, anterior microwear texture signals remain constant.



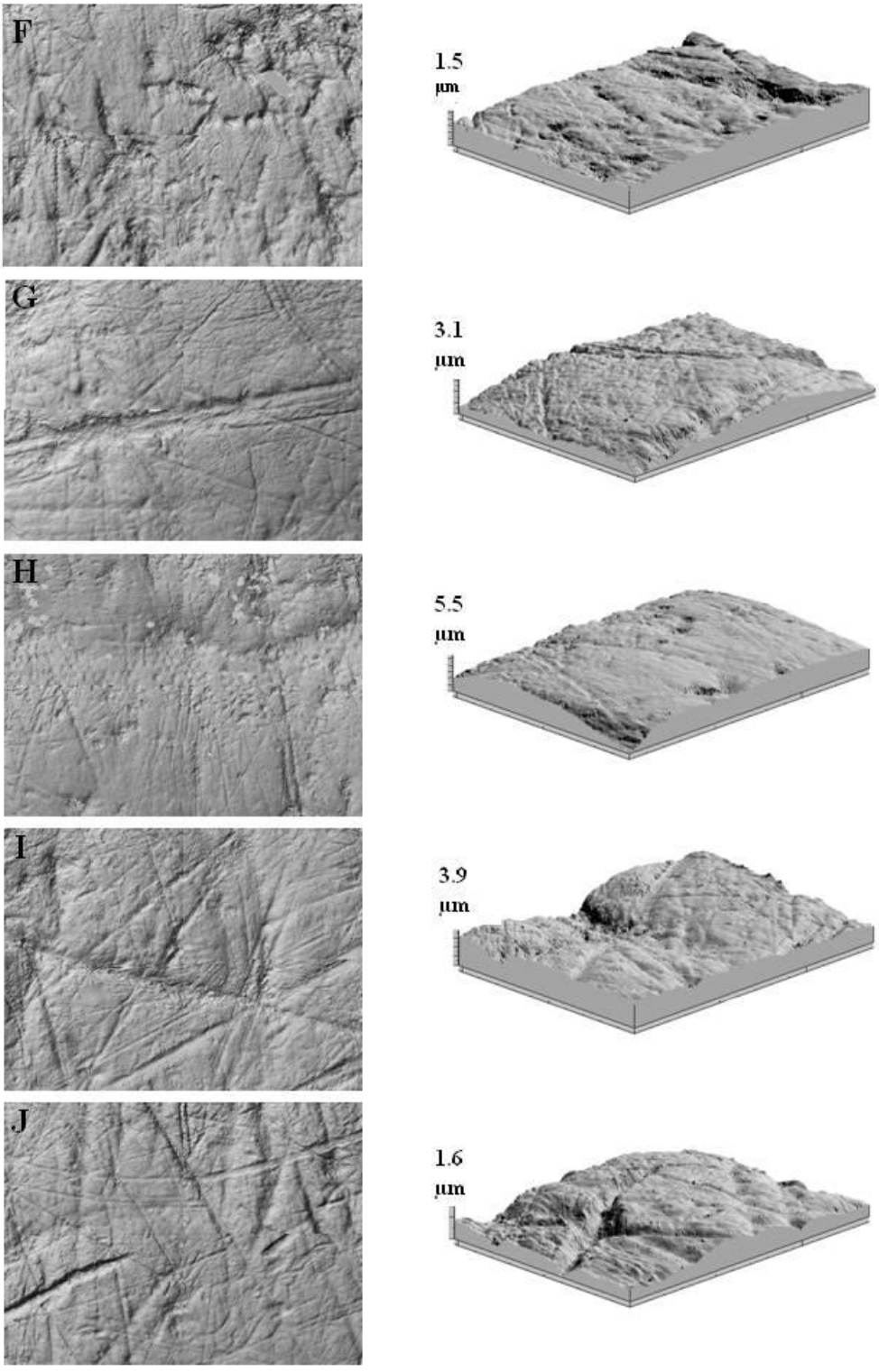


Figure 6.1: Point cloud examples of the AMH individuals. A= Aurignac 4176, B=Brassempouy BR94, C=Dolní Věstonice 13, D=Lachaud 4, E=Lachaud 5, F=Langerie-Basse, G=Les Rois 3, H=Ohalo 2, I=Skhūl 4, J=Vindija 22.1.

MANOVA					
		Test statistic	***F***	**df**	***p***
Tooth Type	Pillai's Trace	0.39	2.21	6, 21	0.08
	Wilks' λ	0.61	2.21	6, 21	0.08
	Holtelling's Trace	0.63	2.21	6, 21	0.08
Jaw	Pillai's Trace	0.23	1.06	6, 21	0.42
	Wilks' λ	0.77	1.06	6, 21	0.42
	Holtelling's Trace	0.30	1.06	6, 21	0.42
Tooth Type * Jaw	Pillai's Trace	0.30	1.50	6, 21	0.23
	Wilks' λ	0.70	1.50	6, 21	0.23
	Holtelling's Trace	0.43	1.50	6, 21	0.23

Table 6.2: Results of the two-factor MANOVA testing differences in microwear textures between incisor type and jaw. Analyses performed on ranked data.

Further statistical tests are completed to determine more specific information about variation in the central tendencies and distribution variance of the AMH sample. First, Levene's Test of Equality of Error Variances was calculated on raw data to determine whether there was homogeneity of variance. There are significant differences in heterogeneity 3x3 and 9x9 by climate, location, and OIS number, as well as in scale of maximum complexity by climate. This indicates the homogeneity of variance assumption was not met. Because there were differences in variance in all three factors, the raw data were rank transformed to mitigate assumptions intrinsic in parametric statistical analyses (Conover & Iman, 1981).

As with the Neandertal study, a three-factor MANOVA was to be calculated on ranked microwear texture data, with climate, location, and OIS number as the factors, and the texture attributes as dependent variables. However, the OIS 5 subcategory, those individuals from the Skhūl site, lack the sample size (n = 3) required for the MANOVA analyses, and would have been excluded. Consequently, to retain the Skhūl individuals, a

two-factor MANOVA, with climate and location as the factors and each texture attribute as dependent variables, was completed on ranked microwear texture data (n = 42). A MANOVA with OIS as a factor was completed separately, and included all individuals except those from Skhūl (n = 39).

No significant differences in central tendencies are found in the overall MANOVA model for climate, location, and OIS number (Tables 6.5 and 6.10). However, as stated above, significant differences in the distribution variance of heterogeneity 3x3 and 9x9 are found for all three factors. The results for each factor will be addressed separately.

Climate

The descriptive statistics for the two climate subcategories, warm-woodland and cold-open-steppe are found in Table 6.3. The Levene's test shows significant differences in distribution variance between the two climate subcategories in their scale of maximum complexity (*Smc*), heterogeneity 3x3 ($HAsfc_9$), and heterogeneity 9x9 ($HAsfc_{81}$) (Table 6.4, Fig. 6.2).

Pairwise comparisons for the distribution variance are unnecessary as only two climate categories exist. For the scale of maximum complexity, the cold-open-steppe anatomically modern humans show significantly higher variance than their warm-woodland counterparts. Moreover, the significant differences in variance for heterogeneity 3x3 and 9x9 can be attributed to the warm-woodland anatomically modern humans' expanded range of heterogeneity values compared with those of the cold-open-steppe individuals. As stated above, there were no significant differences in central tendencies for any of the texture attributes (Table 6.5).

AMH BY CLIMATE: WARM-WOODLAND						
	Asfc	***Smc***	***epLsar***	***Tfv***	***HAsfc9***	***HAsfc81***
Mean	1.30	0.39	0.0032	9012.13	0.74	1.01
Median	1.05	0.27	0.0030	11275.56	0.64	0.78
SD	0.95	0.37	0.0010	5690.59	0.52	0.53
AMH BY CLIMATE: COLD-OPEN-STEPPE						
	Asfc	***Smc***	***epLsar***	***Tfv***	***HAsfc9***	***HAsfc81***
Mean	1.28	1.89	0.0034	9837.39	0.46	0.78
Median	1.05	0.27	0.0032	11685.99	0.41	0.72
SD	0.75	5.18	0.0012	5614.20	0.15	0.28

Table 6.3: Descriptive statistics of the AMH sample by climate. Warm-woodland *n* = 14 and cold-open-steppe *n* = 28.

LEVENE'S TEST BY CLIMATE			
	F	**df**	***p***
Asfc	0.961	1, 40	0.33
epLsar	0.568	1, 40	0.46
Smc	4.483	1, 40	0.04
Tfv	0.024	1, 40	0.88
$HAsfc_9$	9.650	1, 40	0.00
$HAsfc_{81}$	9.642	1, 40	0.00

Table 6.4: Levene's Test results showing significant differences in variance by climate.

MANOVA					
		Test statistic	***F***	**df**	***p***
Climate	Pillai's Trace	.164	1.075	6, 33	.397
	Wilks' λ	.836	1.075	6, 33	.397
	Holtelling's Trace	.196	1.075	6, 33	.397
Location	Pillai's Trace	.430	1.550	12, 68	.128
	Wilks' λ	.616	1.506	12, 66	.144
	Holtelling's Trace	.548	1.462	12, 64	.162
Climate * Location	Pillai's Trace	.000	.	0, 0	.
	Wilks' λ	1.000	.	0, 35.5	.
	Holtelling's Trace	.000	.	0, 2	.

Table 6.5: Two-factor MANOVA with climate and location as factors. Analyses performed on ranked data.

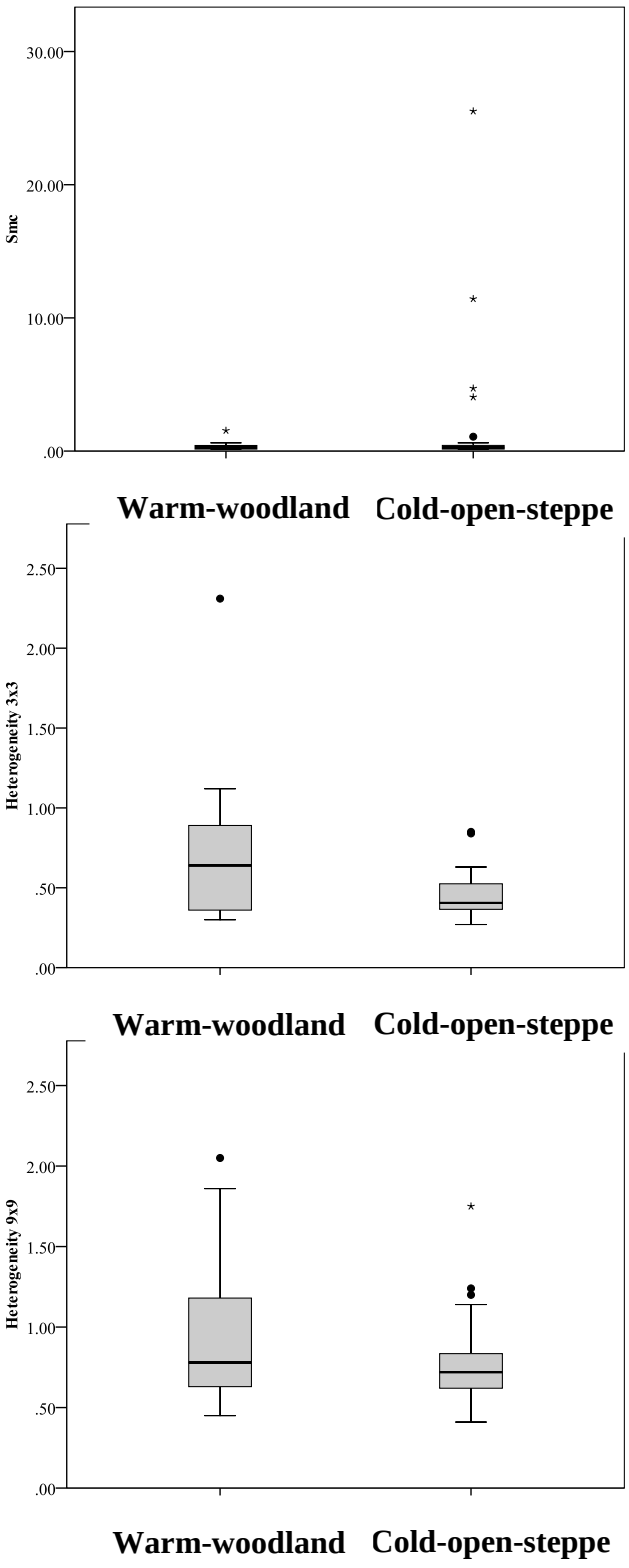


Figure 6.2: Box plots of AMH scale of maximum complexity (*Smc*), heterogeneity 3x3 (*HAsfc*$_9$), and heterogeneity 9x9 (*HAsfc*$_{81}$) by climate.

Location

The descriptive statistics for the three locations, north, central, and south, are found in Table 6.6. The Levene's test indicates significant differences in distribution variance in heterogeneity 3x3 and heterogeneity 9x9 (Table 6.7, Fig. 6.3). Pairwise comparisons are necessary since there are more than two subcategories.

Tukey's HSD pairwise comparisons indicate the southern AMH have significantly greater heterogeneity 3x3 ($HAsfc_9$) distribution variance than the northern and central individuals. Tukey's tests also show that the southern AMH subsample has significantly greater heterogeneity 9x9 ($HAsfc_{81}$) variance than those in the north, and marginally greater variance than those in the central area (Fig. 6.3). As with the climate factor, no significant differences in central tendencies were found in the texture attributes by location (Table 6.5).

AMH BY LOCATION: NORTH						
	Asfc	***Smc***	***epLsar***	***Tfv***	***HAsfc9***	***HAsfc81***
Mean	1.46	0.78	0.0033	7956.21	0.40	0.73
Median	1.47	0.18	0.0024	6466.80	0.36	0.64
SD	0.61	1.59	0.0017	5284.76	0.09	0.23
AMH BY LOCATION: CENTRAL						
	Asfc	***Smc***	***epLsar***	***Tfv***	***HAsfc9***	***HAsfc81***
Mean	1.11	2.13	0.0036	9423.84	0.47	0.77
Median	0.79	0.34	0.0033	11631.48	0.41	0.71
SD	0.79	5.64	0.0010	6157.03	0.15	0.29
AMH BY LOCATION: SOUTH						
	Asfc	***Smc***	***epLsar***	***Tfv***	***HAsfc9***	***HAsfc81***
Mean	1.53	0.28	0.0030	11019.87	0.83	1.12
Median	1.25	0.27	0.0029	12196.07	0.73	0.93
SD	0.95	0.17	0.0010	4521.15	0.56	0.55

Table 6.6: Descriptive statistics of the AMH sample by location. North *n* = 8, central *n* = 23, and south *n* = 11.

LEVENE'S TEST BY LOCATION			
	F	**df**	***p***
Asfc	0.904	2, 39	0.41
epLsar	2.639	2, 39	0.08
Smc	2.718	2, 39	0.08
Tfv	1.848	2, 39	0.17
$HAsfc_{9}$	5.467	2, 39	0.01
$HAsfc_{81}$	5.257	2, 39	0.01

Table 6.7: Levene's Test results of significant differences in variance by location.

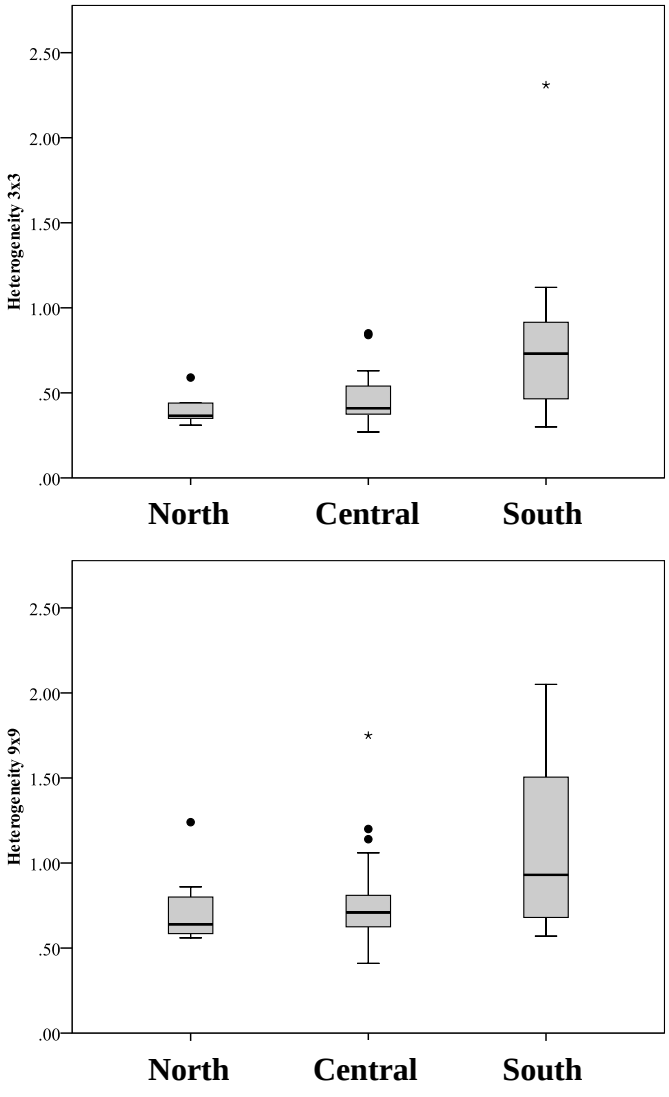


Figure 6.3: Box plots of AMH heterogeneity 3x3 ($HAsfc_{9}$), and heterogeneity 9x9 ($HAsfc_{81}$) by location.

OIS number

The descriptive statistics for each texture attribute with specimens grouped by OIS number are located in Table 6.8. Levene's test indicates significant differences in the distribution variance of heterogeneity 3x3 and 9x9, with the OIS 3 subsample demonstrating signficantly greater distribution variance than those from OIS 2 (Table 6.9, Fig. 6.4). No significant differences are found in central tendencies for any texture attribute grouped by OIS interval (Table 6.10).

AMH FROM OIS 3						
	Asfc	***Smc***	***epLsar***	***Tfv***	***HAsfc9***	***HAsfc81***
Mean	1.23	1.89	0.0035	9188.93	0.53	0.86
Median	0.93	0.27	0.0036	11129.92	0.44	0.70
SD	0.76	5.35	0.0012	4982.08	0.21	0.35
AMH FROM OIS 2						
	Asfc	***Smc***	***epLsar***	***Tfv***	***HAsfc9***	***HAsfc81***
Mean	1.30	0.67	0.0033	9892.46	0.42	0.70
Median	1.07	0.27	0.0031	11740.49	0.39	0.71
SD	0.92	1.08	0.0010	7031.77	0.11	0.18

Table 6.8: Descriptive statistics of the AMH sample by OIS. OIS 3 *n*=13, OIS 2 *n*=26.

LEVENE'S TEST BY OIS NUMBER			
	F	**df**	***p***
Asfc	0.702	1, 37	0.41
epLsar	0.441	1, 37	0.51
Smc	2.738	1, 37	0.11
Tfv	2.380	1, 37	0.13
$HAsfc_9$	7.782	1, 37	0.01
$HAsfc_{81}$	4.786	1, 37	0.04

Table 6.9: Levene's Test results of significant variance by OIS number.

MANOVA					
		Test statistic	***F***	**df**	***p***
OIS	Pillai's Trace	0.08	0.46	6, 32	0.83
	Wilks' λ	0.92	0.46	6, 32	0.83
	Holtelling's Trace	0.09	0.46	6, 32	0.83

Table 6.10: MANOVA results with OIS as factor. Analyses performed on ranked data.

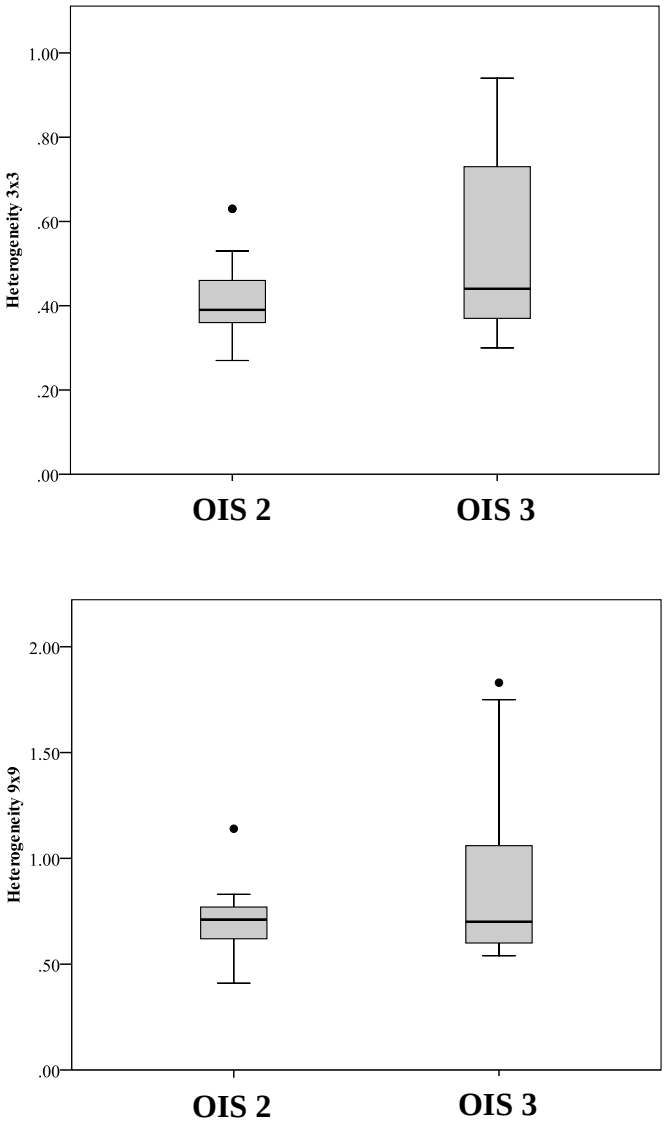


Figure 6.4: Box plots of AMH heterogeneity 3x3 (*HAsfc*$_9$), and heterogeneity 9x9 (*HAsfc*$_{81}$) by OIS number.

Discussion

These data provide evidence for dietary and behavioral strategies of anatomically modern humans, as suggested by significant differences in distribution variance. As with the Neandertal sample, each independent factor will be discussed separately.

Climate

The anatomically modern human (AMH) sample, divided into two climate subgroups of warm-woodland and cold-open-steppe, shows significant differences in distribution variance of scale of maximum complexity, heterogeneity 3x3, and heterogeneity 9x9. The cold-open-steppe AMH subsample shows an expanded range of *Smc* values compared with their warm-woodland counterparts (Fig. 6.2). This difference in variance is most likely due to the four high outlying values found in the cold-open-steppe subgroup, similar to that found with the cold-open-steppe Neandertals. This suggests that these cold-open-steppe AMH had fewer features at a fine scale, which may correspond to very large features.

The warm-woodland AMH subsample shows significantly greater distribution variance than the cold-open-steppe group in both heterogeneity 3x3 and 9x9 (Fig. 6.2). Past research suggests that heterogeneity may be related to dietary and/or environmental abrasive loads, but the signal is likely exacerbated by non-dietary anterior tooth use (Krueger & Ungar, 2010). The warm-woodland AMH show a moderately low mean anisotropy value of 0.0032, (Table 6.3), similar to that of the Tigara from Point Hope, suggesting non-dietary anterior tooth use practices may have been utilized. This premise is strengthened by examining the anisotropy distribution variance of these individuals,

which shows values predominantly within the range of non-dietary anterior tooth use, but also has values above this signal (Fig. 6.5). This indicates that the warm-woodland AMH may have employed some non-dietary anterior tooth use behaviors, but it would have been limited in nature. Perhaps the greater range in heterogeneity 3x3 and 9x9 of the warm-woodland sample denotes a wider range of levels of abrasive exposure than that found in the cold-open-steppe AMH subsample, with the higher range of values representative of the intensification of the signal due to the occurrence of some non-dietary anterior tooth use among the subsample.

Differences in distribution variance aside, there were no significant differences in central tendencies in anterior microwear textures between the climate subcategories. Overall, they show little to no non-dietary anterior tooth use behaviors and moderate-to-high dietary and/or environmental abrasive loads. This homogeneous signal is in stark contrast to that found in the Neandertal sample, which shows significant differences in anisotropy and textural fill volume between the two climate subgroups. Specifically, the cold-open-steppe Neandertals are significantly lower in anisotropy and significantly higher in textural fill volume than the warm-woodland Neandertals. This is probably related to the intensity of tooth use behaviors, in that while the cold-open-steppe Neandertals were likely using their anterior dentition in a focused and concentrated clamping and grasping regimen, perhaps in the production of protective coverings, the warm-woodland Neandertals were not. The lack of differences in the AMH values when specimens are grouped by climate suggests consistency in their behavioral adaptations.

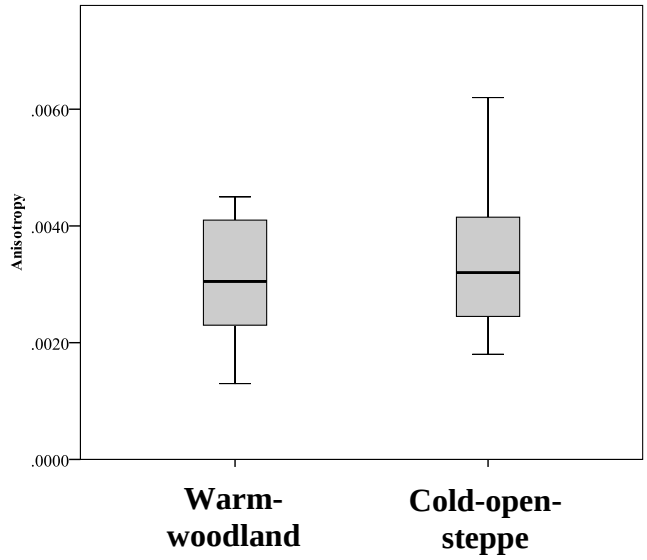


Figure 6.5: Boxplot of the anisotropy distribution variance of AMH by climate.

Location

The AMH sample, divided into three location subgroups, north, central, and south, shows significant differences in distribution variance in heterogeneity 3x3 and 9x9. Specifically, the southern AMH have a significantly greater range of heterogeneity 3x3 values than both the central and northern subgroups (Fig. 6.3). The southern subsample also has a significantly greater range of heterogeneity 9x9 than the northern individuals and a marginally greater range than the central individuals (Fig. 6.3). This reflects the decrease in $HAsfc_{81}$ range from south to central to north.

As described with the climate factor, heterogeneity 3x3 and 9x9 have been used as indicators of abrasive loads, but the signal is intensified if non-dietary anterior tooth use practices are utilized. The greater distribution variance of the southern AMH suggests these individuals were exposed to a wider range of dietary and/or environmental abrasive loads than their central and northern counterparts. However, the low mean

anisotropy value (0.0030) of the southern AMH, similar to that of the Aleut, indicates some non-dietary anterior tooth use practices, which may be exacerbating the heterogeneity 3x3 and 9x9 distribution variance. This idea is strengthened by the anisotropy distribution variance of the southern AMH subsample, which is more constricted, and shows overall lower values, than the central and northern subgroups (Fig. 6.6)

The heterogeneity 9x9 texture attribute is also important in distinguishing the Neandertal sample by location; however, the central tendencies are significantly different, and the distribution variance is not. This is opposite to what was found for the AMH, where the distribution variance is significant, and the central tendencies are not. Perhaps this signals differences in the range of behaviors employed by each hominin. Regardless, the heterogeneity variable seems to be especially useful in distinguishing hominins by location, whether in distribution variance or central tendencies, and appears to be connected to abrasive loads, whether in conjunction with dietary or non-dietary anterior tooth use behaviors.

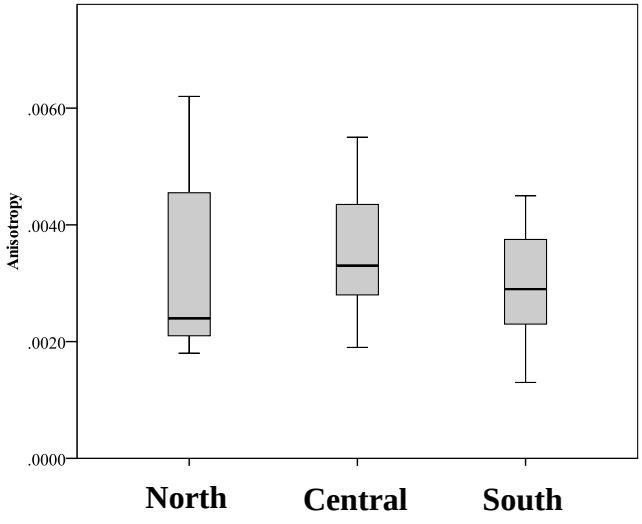


Figure 6.6: Boxplot of the anisotropy distribution variance of AMH by location.

OIS number

The anatomically modern human sample, divided into OIS 3 and 2, shows significant differences in distribution variance of heterogeneity 3x3 and 9x9. Specifically, the OIS 3 AMH shows a greater range of values in both variants of the heterogeneity attribute than those from OIS 2 (Fig. 6.4). Since differences heterogeneity values may be caused by differences in non-dietary anterior tooth use, an examination of these values is also warranted.

Both the OIS 3 and 2 subsamples have anisotropy values that fall within the range of modern human samples that use their anterior dentition for dietary purposes only. Indeed, the OIS 3 and 2 mean values are 0.0035 and 0.0033 respectively, most similar to the Chumash and Fuegian bioarchaeological samples.

Therefore, the heterogeneity values may be interpreted as resulting from abrasive loads alone. Consequently, the significantly greater variance of the OIS 3 AMH suggests these individuals were exposed to a wider range of dietary and/or environmental abrasive loads than their OIS 2 counterparts.

Heterogeneity 3x3 and 9x9 are also important in distinguishing Neandertals by OIS interval, although, just as with the location factor, the Neandertal central tendencies were significantly different, not the distribution variance. Perhaps this indicates differences in the range of behaviors employed by these two hominins. The significant differences were also attributed to not only high abrasive loads, but non-dietary anterior tooth use behaviors of the OIS 4 Neandertals, whereas non-dietary behaviors are not considered a contributing factor to the AMH sample. Further, the anterior microwear texture analyses with AMH specimens grouped by both location and OIS strongly

suggests that the heterogeneity variable and its variants are important in recognizing differences in both types of hominins.

OIS 3 anatomically modern humans

As discussed in Chapter 5, OIS 3 is often associated with rapid fluctuations of global climate and a continuous environmental deterioration with the approach of the last glacial maximum. This climate change is also implicated in the demise of the Neandertals. An analysis of the overall OIS 3 Neandertals indicates an elimination of non-dietary anterior tooth use behaviors, a severe deviation from the other OIS intervals. However, a breakdown of the OIS 3 Neandertals by climate reveals that the cold-open-steppe individuals of OIS 3 were engaging in intense and focused non-dietary anterior tooth use behaviors, perhaps those associated with the production of protective coverings. On the other hand, the warm-woodland Neandertals of OIS 3 have a completely different signal, with high anisotropy values that indicated only dietary use of the anterior dentition.

It may be beneficial to also examine the OIS 3 anatomically modern human sample to look for an effect of climate on anterior dental microwear texture signals. Overall, the OIS 3 AMH values provide no evidence for non-dietary anterior tooth use behaviors, and indicate moderately high abrasive loads (Table 6.11). When this sample is broken down by climate, the signal remains the same, with no evidence for the use of their anterior dentition as a tool, and moderate-to-high exposures to dietary and/or environmental abrasive loads (Table 6.11). This suggests that during the chaotic climate

oscillations associated with OIS 3, the AMH were engaging in similar anterior tooth use behaviors, regardless of climate.

AMH FROM OIS 3						
	Asfc	***Smc***	***epLsar***	***Tfv***	***HAsfc9***	***HAsfc81***
Mean	1.23	1.89	0.0035	9188.93	0.53	0.86
Median	0.93	0.27	0.0036	11129.92	0.44	0.70
SD	0.76	5.35	0.0012	4982.08	0.21	0.35

AMH FROM OIS 3: WARM-WOODLAND						
	Asfc	***Smc***	***epLsar***	***Tfv***	***HAsfc9***	***HAsfc81***
Mean	1.30	0.34	0.0036	9613.93	0.68	0.97
Median	0.97	0.27	0.0038	11275.56	0.73	0.90
SD	1.01	0.18	0.0008	4994.69	0.23	0.42

AMH FROM OIS 3: COLD-OPEN-STEPPE						
	Asfc	***Smc***	***epLsar***	***Tfv***	***HAsfc9***	***HAsfc81***
Mean	1.20	2.57	0.0035	9000.03	0.47	0.81
Median	0.93	0.27	0.0033	9473.57	0.42	0.66
SD	0.64	6.36	0.0013	5109.47	0.16	0.32

Table 6.11: Descriptive statistics for the OIS 3 AMH. Top data are for the OIS 3 AMH as a whole (*n* =26), center data are for the warm/woodland individuals (*n* = 8), and bottom data (*n* = 18) are for the cold-open-steppe AMH.

Conclusion

Although there are no significant differences in AMH central tendencies by climate, location, or OIS number, differences in distribution variance allow for some inferences to be made. Specifically, all three factors show significant differences in their heterogeneity 3x3 and 9x9 distribution variance. The heterogeneity variable has been linked to abrasive loads in previous analyses (Krueger & Ungar, 2010), but is exacerbated by non-dietary anterior tooth use practices. However, the AMH sample shows little-to-no evidence for non-dietary anterior tooth use behaviors, so this factor

would likely have been at best marginally influential in the AMH heterogeneity variance differences.

An in-depth analysis of the OIS 3 AMH by climate reveals the same pattern of homogeneity in microwear texture signals. Specifically, both the cold-open-steppe and warm-woodland AMH of OIS 3 were likely not using their anterior dentition as a tool, clamp, or third hand, and were exposed to moderate-to-high abrasive loads. This homogeneous signal is different from that found in the Neandertal OIS 3 subsamples by climate, with the cold-open-steppe Neandertals demonstrating an intense and focused regimen of non-dietary anterior tooth use behaviors, perhaps in the continuous production of protective coverings.

The differences in inferred non-dietary anterior tooth use practices between the cold-open-steppe OIS 3 Neandertals and cold-open-steppe OIS 3 AMH are striking, as both hominin groups would have required protective coverings during this time. Indeed, evidence exists for the production of hides for such purposes for both the Neandertals and AMH (Anderson-Gerfaud, 1990; Hardy, 2004; Valensi & Psathi, 2004; West, 2001), with demand increasing steadily as the mean annual temperature decreased. So, what can account for the difference in non-dietary anterior tooth use between these two hominins?

Perhaps differences in tool industries are responsible. Indeed, the advent of the Upper Paleolithic is often associated with an increase in tool sophistication and variability, including, for the first time, the production and use of needles (Shea, 2011). This development in tool complexity and style is often used as a signal of the advanced cognitive and behavioral abilities of the encroaching anatomically modern humans; however, the Neandertal and AMH toolkits may simply and solely represent different

adaptive solutions to the same problem (Shea, 2011). Regardless, perhaps the lack of non-dietary anterior tooth use found not only within the cold-open-steppe OIS 3 AMH, but throughout the AMH sample as a whole, is evidence that this hominin had at its disposal a more extensive toolkit that released the anterior dentition from non-dietary use.

CHAPTER SEVEN: CONCLUSIONS

Goals

Several important goals are realized with the completion of this project. First, fossil studies to use dental microwear texture analysis to date have only focused on premolars and molars. Initial studies of incisors suggest bioarchaeological samples can be distinguished on the basis of I^1 microwear textures (Krueger & Ungar, 2010), and this study confirmed or revised initial interpretations, with the expansion from five to thirteen different bioarchaeological human samples (n=257) ranging from high-arctic Alaska to Tierra del Fuego.

The successful completion of this first goal leads to the second, which is the development of a Neandertal anterior dental microwear texture database, with sixty-five adult individuals represented. This extensive collection not only allows for comparisons never before possible on anterior microwear, but also the recognition of differences in Neandertal anterior tooth use strategies by climate, location, and OIS intervals. Moreover, it is demonstrated that dental microwear texture signals are homogeneous between anterior tooth type (central incisor, lateral incisor, and canines) and jaw (maxilla and mandible), at least for the samples considered here. This provides evidence for texture signal consistency among the front teeth, and will presumably allow for future research to expand their sample sizes.

The third goal is to produce a substantial sample of anatomically modern human anterior dental microwear textures. Decades of studies have compared Neandertals to the incoming modern humans, usually in the context of the latter possessing more advanced cognitive and behavioral adaptability. An in-depth examination of their anterior dental

microwear textures documents differences in distribution variance by climate, location, and OIS interval, though their homogeneous central tendencies reflect the stability in their adaptive strategies related to anterior tooth use. Statistical tests also fail to find significant differences in their texture signals by anterior tooth type and jaw, further suggesting the ability to combine samples.

The fourth and final goal is the comparison of Neandertals and anatomically modern humans. Decades of research on these two hominins has suggested their behavior and adaptations were intrinsically different. Specifically, it has been suggested that anatomically modern humans were likely able to survive the changing climates of OIS 3 because they were cognitively and behaviorally advanced. An examination of the OIS 3 Neandertals and anatomically modern humans suggests variation by climate, but only within the former sample. The anatomically moderns of OIS 3 are consistent in microwear textures across climates, while Neandertals in cold-open-steppe environments of OIS 3 are different from those Neandertals in warm-woodland climates of OIS 3.

Brief summaries and concluding remarks for each goal are presented here individually, with a discussion of the fourth goal included within each hominin summary.

Bioarchaeological sample

Use of dental microwear texture analysis

Preliminary studies suggested that dental microwear texture analysis could distinguish bioarchaeological groups by their incisor microwear textures (Krueger & Ungar, 2010). However, the suite of texture attributes that had been most useful in molar microwear texture studies was limited in applicability for incisor microwear textures.

Namely, anisotropy (*epLsar*), textural fill volume (*Tfv*), and heterogeneity 3x3 ($HAsfc_9$), varied significantly among the initial five samples (Krueger & Ungar, 2010).

Anisotropy reflects the practice of non-dietary or dietary anterior tooth use, in that low values corresponded to the former, and high values to the latter. Textural fill volume corresponds to either high magnitude loading of the anterior teeth or abrasive particle density or size, depending on the signal presented by the anisotropy value. Finally, heterogeneity 3x3 is used as a proxy for dietary and/or environmental abrasive loads.

With the expansion of the modern human comparative samples from five to thirteen, many of these interpretations remained correct; however, revisions to a few hypotheses presented in Krueger & Ungar (2010) were made, and additional interpretations were warranted for the remaining texture attributes, complexity (*Asfc*), scale of maximum complexity (*Smc*), and heterogeneity 9x9 ($HAsfc_{81}$), that evinced significant variation. These data indicate the usefulness of dental microwear texture analysis in characterizing bioarchaeological groups by their incisor microwear signatures. They also provide evidence for this technique's ability to document subtle differences that may have been lost with observer measurement error in traditional scanning electron or light microscopy-based analyses.

Sample selection

The bioarchaeological samples were selected for analysis because of their wide-ranging differences in climate types, dietary and/or environmental abrasive loads, subsistence strategies, and variety of non-dietary anterior tooth use behaviors. The last factor was especially important to document, as it is the most commonly cited

explanation for the unique Neandertal anterior dental wear pattern. The five arctic samples, ranging from low to high latitudes, were specifically selected given past comparisons of the anterior dental wear between Alaskan Eskimo and Canadian and Greenland Inuit populations on the one hand and Neandertals on the other.

Lastly, several other bioarchaeological samples, including the Andamanese, Chumash, and Fuegians, were included in this analysis because they showed a range of climate type, abrasive loads, and non-dietary anterior tooth use behaviors not found in the other samples. However, they were also included to provide complementary analyses to molar microwear of studies of Neandertals, which also included the Aleut, Ipiutak, and Tigara (El Zaatari, 2007). Thus, both incisor and molar microwear textures exist for these six samples, and allow for future comparisons of microwear textures between tooth types that differ in both morphology and function.

Results and implications

The analysis of the thirteen bioarchaeological samples showed significant variation, and the assemblage of texture variables allowed for a more complete picture of incisor microwear textures to be presented. For example, more than half of the samples are known to have engaged in non-dietary anterior tooth use behaviors, and all of these groups had low anisotropy values. This reconfirms the initial hypothesis presented in Krueger & Ungar (2010). Further, different types of non-dietary anterior tooth use behaviors, such as clamping, grasping, softening fibers, or tool retouching, could be distinguished from the textural fill volume values of these samples. This garners support

for the original hypothesis presented in Krueger & Ungar (2010) in which textural fill volume could indicate amount and magnitude of anterior dental loading.

For example, the Ipiutak and Nunavut Territory demonstrated similar texture values across the board, but specifically, both had extremely low anisotropy and high textural fill volume values. This pattern of values reflects their similarly intense regimen of clamping and grasping with their anterior dentition in the preparation of caribou hides for the production of clothing, boots, boat skins, and for trade. Likewise, the low anisotropy and moderate textural fill volume of the Prince Rupert Harbour, BC sample signified the documented labret use and basketry production of this population. Both the Aleut and Tigara samples had moderately low anisotropy and moderately high textural fill volume values, matching their comparable pattern of their occasional use in grasping and clamping activities. Lastly, the Illinois Bluff and Andamanese displayed low anisotropy and low textural fill volume, a combined signal indicating the use of the anterior dentition in tool production and retouching.

Those samples without non-dietary anterior tooth use demonstrated high anisotropy values, and their textural fill volume values were originally hypothesized to indicate abrasive particle density or size in Krueger & Ungar (2010). Although the majority of the samples in this expanded study fit this pattern, the Chinese immigrants, Amarna, and Arikara samples did not. A suggested revision to the original hypothesis includes the role that food fracture properties play on incisor microwear textures; that is, if food items with highly elastic properties are consumed, or if no incisal preparation is required, lower textural fill volume values may result. Further testing will no doubt allow for continued analysis of this revised idea.

Data from Krueger & Ungar (2010) suggested that dietary and environmental abrasives played a role in heterogeneity 3x3 variation among samples. As detailed in Chapter 3, heterogeneity measures texture variability across the enamel surface. This follows from the idea that the presence of a variety of abrasive types and sizes, either wind-borne or adherent on food items during incising, would leave a variety of differently sized microwear features, creating high variability of textures across the enamel surface. However, the heterogeneity 3x3 variation among the expanded dataset in Chapter 4 did not fully support this original hypothesis. In fact, significant variation in heterogeneity 3x3 was found within those samples that are recorded as having similarly high exposure to abrasive types and sizes; however, the difference was found in the type of non-dietary anterior tooth use.

Specifically, high heterogeneity values seem to correspond to high abrasive exposure, as predicted by Krueger & Ungar (2010), but non-dietary anterior tooth use appears to exacerbate the signal. For example, both the Ipiutak and Nunavut Territory groups had significantly higher heterogeneity values than the other samples, and this is not likely due to abrasive loads alone. Therefore, it was proposed that their intense regimen of non-dietary anterior tooth use behaviors intensified the signal. A similar pattern was found with the fine-scale variant of heterogeneity, 9x9, although this will require further testing for confirmation.

Likewise, the complexity variable was found to be positively correlated to heterogeneity 9x9, as both of these values changed in tandem. Not significant in Krueger & Ungar (2010), an initial hypothesis for the complexity variation found in the expanded dataset was a combination of both abrasive loads and non-dietary anterior tooth use

behaviors. Further analyses can hopefully provide additional information about this texture attribute signal, as well as its connection to other attributes.

The incisor microwear texture analysis of these thirteen bioarchaeological samples suggest the association of several microwear attributes with specific subsistence and behavioral strategies, especially in regards to different variations in non-dietary anterior tooth use practices and abrasive loads. The data presented here offer confirmation of previous hypotheses put forth by Krueger & Ungar (2010), and also provide the opportunity for revised models for those data that did not conform to original ideas. Moreover, initial hypotheses could be presented for those texture attributes that did not provide significant results in prior analyses. Last, and most important to this study, is that these data can be used to confirm, revise, and generate hypotheses concerning dietary and subsistence strategies of fossil hominins.

Arctic samples as a proxy for Neandertals

Early studies describing the unique anterior dental wear pattern found on some Neandertals specimens, such as La Ferrassie I and II and Shanidar I, suggested several different possible causes. The most commonly proposed etiology was the use of the anterior dentition as a clamp, tool, or third hand (Brace, 1967, 1975; Brace et al., 1981; Ryan, 1980). This was inferred by analogy with Alaskan Eskimo and Canadian and Greenland Inuit populations which used their front teeth in this manner. Since these early studies, comparisons between Neandertals and arctic populations have become commonplace, with analogy suggesting everything from carnivorous dietary habits to the cold-adapted body form; and thus, it was important to use arctic samples in this analysis.

However, past Neandertal research has used a wide variety of arctic samples in their analyses, and usually includes a limited discussion about the population's background or circumstances. It is important for paleoanthropologists to appreciate the subsistence, technological, linguistic, and genetic differences that exist within the arctic. An in-depth understanding of these differences can facilitate comparisons. The two high-arctic samples from Point Hope, the Ipiutak and Tigara, provide an appropriate example.

The Ipiutak and Tigara both occupied the Point Hope spit, located on the northwest coast of Alaska, but at different times. The Ipiutak were located there before the Tigara, and were summer residents of Point Hope, suggested to have followed the caribou migration to the coast for the summer months, and returning to the interior during the rest of the year (Larsen & Rainey, 1948). The dependence on caribou and not whale hunting at Point Hope was hypothesized from the lack of harpoons and the overabundance of archery artifacts found in the archaeological assemblages (Larsen & Rainey, 1948).

The Tigara, on the other hand, lived at Point Hope all year, and were mostly whale hunters (Larsen & Rainey, 1948; Burch, 1981; Foote, 1992). Indeed, many different types and varieties of whale harpoon heads were found in the excavations, as well as ethnographic reports from early American and European explorers who documented this reliance (Beechey, 1831; Foote, 1992). Moreover, Point Hope has been referred to as one of the best whaling locations in the world (Burch, 1981). Until this study, differences in dietary strategies between the Ipiutak and Tigara had only been hypothesized.

Incisor microwear texture analysis of the Ipiutak and Tigara showed significant differences in all five texture attributes, providing support for the archaeological evidence that suggested different diets. Namely, the Ipiutak had extremely low anisotropy and high textural fill volume, values consistent non-dietary anterior tooth use and high magnitude loading of the anterior dentition. In fact, this signal indicates an intense regimen of clamping and grasping activities, most like related to the time-consuming, arduous, and continuous task of caribou hide preparation for clothing and trade purposes.

On the other hand, the Tigara had moderately low anisotropy and moderately high textual fill volume, a pattern consistent with non-dietary anterior tooth use, but only moderate loading. While the values of these two attributes indicate clamping and grasping activities, it is not to the degree as that of the Ipiutak. This is consistent with ethnographic reports of the Tigara processing sea mammals, such as walrus and seal, that required less preparation, and either less anterior tooth use, or none at all (Foote, 1992). The heterogeneity, complexity, and scale of maximum complexity were also higher for the Ipiutak, providing evidence for high abrasive loads, as well as confirming the presence of non-dietary anterior tooth use behaviors. Clearly, the Ipiutak and Tigara relied on different anterior tooth use practices, suggesting both distinctions in subsistence and other behavioral adaptations.

Moreover, the Ipiutak texture values corresponded nearly identically to those of the Nunavut Territory, located thousands of miles away. The Tigara sample was most similar to that of the Aleut, located in an oceanic, low-arctic area. Therefore, even though the two high-arctic groups, the Ipiutak and Tigara, lived at the exact same location, they were extremely different in their adaptations. This should provide a

cautionary tale for future Neandertal studies, because differences in subsistence and tooth use behaviors exist across the arctic, and using arctic samples interchangeably, without recognizing each group's distinctions, can lead to inaccurate inferences of Neandertal behavior given inappropriate analogies.

Neandertal sample

The primary focus of this project was to understand Neandertal anterior dental wear. Past research has only posited singular reasons, such as compensation for missing hands (Stewart, 1959), excessive mastication of grit-laden foods (Puech, 1979, 1981), or non-dietary anterior tooth use practices (Brace 1967, 1975; Ryan, 1980; Brace et al., 1981). While these studies were important in determining possible factors, they failed to incorporate the variety of wear-causing variables into one interpretive model. Moreover, methodological challenges hindered concrete results. Thus, the aim of this project was to create a framework that encompassed the possible variables that affect anterior dental wear, and assess those variables within a methodological context that is both objective and repeatable.

This framework has allowed a large volume of data to be collected, factors to be assessed, and interpretations to be made. Neandertal anterior dental microwear signatures varied by climate types, locations, and OIS interval and microwear differences are likely due to variation in Neandertal dietary and behavioral strategies. First, Neandertal subsamples differed significantly by climate in both the distribution variance and central tendencies.

The cold-open-steppe Neandertals had more constricted, lower anisotropy and more constricted, higher textural fill volume values that those in the warm-woodland

subsample. In fact, the cold-open-steppe Neandertal values corresponded closely to those of the Ipiutak and Nunavut Territory bioarchaeological samples, both of which employed an intense non-dietary anterior tooth use regimen associated with continuous and concentrated caribou hide preparation. It is suggested that the cold-open-steppe Neandertals were utilizing a similar regimen as that of the Ipiutak and Nunavut Territory samples, perhaps as an adaptation to survive in the harshly cold environment.

On the other hand, the moderately low anisotropy and moderately high textural fill volume values of the warm-woodland Neandertals were similar to those of the Tigara. This suggests that the warm-woodland Neandertals likely used their anterior dentition in non-dietary behaviors, but probably not nearly as frequently or intensely as their cold-open steppe counterparts. Also, the wide distribution variance found in this subsample suggests they most likely engaged in a wider array of anterior tooth activities, perhaps due to an increased availability of food items, such as plant and marine resources found in warmer climates.

The Neandertal sample also differed significantly in heterogeneity 9x9 and complexity by location. The heterogeneity variable has been identified as being a reasonable proxy for abrasive loads (Krueger & Ungar, 2010), and the complexity variable seems linked to heterogeneity. Both are evidently affected by both dietary and environmental abrasive loads and non-dietary anterior tooth use behaviors. Considering this interpretation, it is interesting to note that the northern subsample demonstrated significantly and marginally higher 9x9 values than the southern and central Neandertals, respectively, and signficantly higher complexity values than the southern and central subgroups. This suggests the northern Neandertals were exposed to a greater amount of

dietary and/or environmental abrasive loads than the other subgroups; however, the low anisotropy values of the northern Neandertals also suggests that non-dietary anterior tooth use behaviors may be exacerbating the signal.

The Neandertal sample varied significantly in textural fill volume, heterogeneity 3x3, and heterogeneity 9x9 when grouped by OIS interval. Differences were found between OIS 6/5 and OIS 4 and the other intervals. First, OIS 6/5 had significantly lower *Tfv* values than all other intervals. Comparisons with the bioarchaeological comparison samples show that the OIS 6/5 Neandertals are similar in anisotropy and textural fill volume values to the Prince Rupert Harbour sample. This group utilized their anterior dentition in basketry production, and also wore labrets. Perhaps the *Tfv* values of the OIS 6/5 Neandertals can be attributed to similar behaviors, or at least behaviors that leave similar microwear.

Second, the OIS 4 Neandertals were signficantly higher in heterogeneity 3x3 and 9x9 than those from OIS 6/5. The OIS 4 subsample was also marginally higher in heterogeneity 9x9 than OIS 3. Heterogeneity may be associated, as stated above, with abrasive loads, but the signal might be accentuated by non-dietary anterior tooth use practices. Since the OIS 4 Neandertals showed low anisotropy values, the heterogeneity differences shown here can be attributed to both abrasive loads and non-dietary anterior tooth use practices.

Lastly, a closer examination of the OIS 3 Neandertals was warranted, as these individuals may provide insights into the circumstances surrounding the extinction of this hominin. While the overall microwear texture signature, especially the high anisotropy values, deviated from the signature seen in intervals that preceded OIS 3, it was only by

parsing this interval by climate that behavioral adaptations were found. Specifically, the mean anisotropy value of the cold-open-steppe Neandertals of OIS 3 was exceedingly low, which, coupled with the high textural fill volume mean, suggests these individuals were participating in heavy non-dietary anterior tooth use behaviors. Conversely, the warm-woodland Neandertals of OIS 3 had very high anisotropy and high textural fill volume means, suggesting only dietary use of the anterior dentition, coupled with high abrasive loads.

It is proposed that this is an indication of very different adaptive strategies during the turbulent, oscillating, and changing climate of OIS 3. A preliminary interpretation is that as the climate changed, the cold-open-steppe Neandertals were preparing hides, likely for the production of protective coverings. These protective coverings would have become more and more in demand as the climate cooled, encouraging an intense clamping and grasping regimen. An increased anterior tooth sample size of cold-open-steppe Neandertals from OIS 3 would help to identify continuity or variance from this initial pattern and allow for confirmed or revised interpretations. Moreover, cutmark and microwear analyses of Neandertal faunal and lithic assemblages, respectively, accumulated during OIS 3 from these cold-open-steppe sites may provide complementary datasets to confirm or refute this idea.

On the other hand, the initial interpretation of the warm-woodland Neandertals of OIS 3 is that these individuals did not need to focus on the same intense regimen as their cold-open-steppe counterparts. Instead, the need for protective coverings was most likely limited given their climate, and they also probably benefited from a wider range of resource availability, such as plant and marine foods, that comes with warmer conditions.

Just as with the cold-open-steppe individuals, an increase anterior tooth sample size would help to sustain these preliminary ideas. Moreover, the continuation of studies examining Neandertal plant food exploitation would surely help to justify these claims.

Anatomically modern human sample

The inclusion of anatomically modern humans to this study helped to identify differences in dietary and behavioral strategies between this hominin and those of Neandertals. Although no significant differences were found in central tendencies by climate, location, or OIS number, differences in distribution variance in all three factors did allow for inferences to be made. Specifically, the distribution variance of heterogeneity 3x3 and 9x9 differed in all three factors. The heterogeneity variable, as discussed above, is linked to abrasive loads, but the signal is apparently intensified by non-dietary anterior tooth use behaviors. Since the AMH sample showed little evidence for non-dietary anterior tooth use practices, this factor would likely have had only marginally influence, and the heterogeneity variance differences can be predominantly attributed to dietary and/or environmental abrasives.

However, the homogeneity of the AMH signals, regardless of factor, suggests that anterior tooth use behaviors were not affected by climate, location, or OIS interval. In fact, even an in-depth examination of the OIS 3 AMH by climate shows the same general signal of only dietary use of the anterior dentition, along with moderate-to-high abrasive loads. This differs greatly from the signal of the OIS 3 Neandertals by climate, and also suggests that the AMH were more stable in their behavioral strategies. Moreover, it also suggests that on a general level, AMH did not use their anterior dentition as a clamp, tool, or third hand very often, and did not use their anterior teeth in this manner at all during

OIS 3. This is consistent with archeological evidence that suggests the AMH had at their disposal a more variable or extensive toolkit, one that may have relaxed pressures on the anterior dentition for performing the tasks they did for Neandertals (Shea, 2011).

Comparing these data to past Neandertal and AMH dental microwear analyses

Past Neandertal and AMH dental microwear analyses, including interproximal, buccal, occlusal, and labial studies, have provided relevant information and interpretations of both the posterior and anterior microwear signatures. This labial study of Neandertal and AMH anterior dentition offers additional data and interpretations, and should be placed into context with earlier research.

Past interproximal wear research has focused on artificial grooves found on some Neandertal posterior and anterior teeth (Frayer & Russell, 1987; Lalueza et al., 1993; Egocheaga et al., 2004; Estalrrich et al., 2011). While some of these studies have suggested that the grooves may have been formed from toothpick use (Frayer & Russell, 1987; Lalueza et al., 1993), others have interpreted these wear features as a consequence of biomechanical stress due to the mastication of grit-laden, hard plant foods (Egocheaga et al., 2004). A different study offered another interpretation, in that the grooves may have been caused from dietary or paramasticatory behaviors (Estalrrich et al., 2011).

Interproximal grooves are large enough to be seen with the naked eye, and are usually examined at low magnification with a light microscope. Therefore, the scale at which these features are found is much more coarse than the scale at which the present study was completed. No interproximal grooving was recorded on the high-resolution casts of the individuals used in this study, and, likewise, no evidence was found to support the idea of toothpick use in these individuals. However, this could be a product

of the type of teeth analyzed, as most of the grooves are located on the posterior teeth. Regardless, there was evidence to support high bite force and paramasticatory behaviors, and perhaps these activities not only created fine-scale features, but also contributed to the coarse-scale interproximal grooving.

Buccal microwear analyses have also been completed on Neandertal and AMH dental samples. Buccal microwear studies examine striations or scratches found on the buccal sides of posterior teeth (Lalueza & Pérez-Pérez, 1993; Lalueza et al., 1993,1996; Pérez-Pérez et al., 2003). Past research has correlated striation length, orientation, and density to different types of diet, such as meat and plants, under the premise that differences in these striation features correlate to differences in dietary and/or environmental abrasive loads (Pérez-Pérez, 2004). Past analyses have suggested that Neandertals relied on a mixed, plant-based, and abrasive diet (Lalueza et al., 1993), a diet heavily dependent on meat (Lalueza & Pérez-Pérez, 1993; Lalueza et al., 1996), and a mixed diet of plants and meat, with a heavier reliance on plants in cold climates, and meat in warm (Pérez-Pérez et al., 2003). Upper Paleolithic individuals have also been examined, with their buccal microwear signatures suggesting a more abrasive, plant-based diet (Lalueza et al., 1996).

The analyses presented here support the notion that Neandertals may have differed in their abrasive loads by location and in their diet by climate. However, the analysis from the data here support the hypothesis that cold-open-steppe Neandertals were relying on animal-based resources, whereas those from warm-woodland climates were perhaps able to relax non-dietary anterior tooth use behaviors, and exploit a wider range of dietary resources, perhaps plant- and marine-based. The analysis of the AMH

here supports the hypothesis that these individuals were exposed to differences in abrasive loads by climate, location, and OIS.

Occlusal microwear analyses of Neandertal and AMH have shown indications of differences within and between these hominins as well. Using dental microwear texture analysis, El Zaatari (2007) demonstrated variation in texture signatures by climate. Specifically, European Neandertals in cold, open steppe climates had lower complexity values than those in warm, woodland climates. This was interpreted as a higher abrasive load for the latter, most likely due to a wider plant resource base, and a lower abrasive load for the former, perhaps due to a higher reliance on meat resources (El Zaatari, 2007).

These results are congruent with those presented here, in that there were indications of differences in microwear textures by climate, with the cold-open-steppe Neandertal signal interpreted as the use of meat resources in non-dietary anterior tooth use behaviors , and the warm-woodland Neandertal signature showing evidence of an expanded resource base, perhaps related to the availability of more plant and marine resources. Differences in abrasive loads were not found by climate, but by location, and the highest abrasive loads were found in the north, with a gradient of lower values for the central and southern locations. However, non-dietary anterior tooth use behaviors are hypothesized to exacerbate the abrasive load signal, and this could be acting as noise in the abrasive load signal.

The early Upper Paleolithic sample showed a wider range of complexity values, which was suggested to indicate the range of dietary breadth (El Zaatari, 2007). While these values were similar to those of the northern and central European Neandertals, they

were signficantly different from those of the southern Neandertals (El Zaatari, 2007). This was interpreted as the latter having a more diverse diet.

The present analyses found significant differences in AMH heterogeneity 3x3 and 9x9 distribution variance by climate, location, and OIS, supporting differences in abrasive loads, not dietary preferences, in all three factors. Moreover, while the southern Neandertals were suggested to have a more diverse diet than those Neandertals in the north or central areas, there were no indications of significant differences between the AMH and southern Neandertals. However, these differences in data are more likely a benefit of using teeth with different morphology and function, and when combined, can present a more complete picture of Neandertal and AMH dietary and behavioral adaptations.

Last, labial studies of the anterior teeth have provided the most applicable data to the present analysis. The excessive labial-lingual wear and/or large striations found on the labial surfaces of anterior teeth have most often been attributed to non-dietary anterior tooth use behaviors. More specifically, the "stuff and cut" scenario, in which Neandertals were hypothesized to have cut a piece of meat close to their lips, sometimes leaving large, stone-tool cutmarks on the labial surface, has been examined (Ryan, 1980; Lalueza Fox & Frayer, 1997; Bax & Ungar, 1999).

The first Neandertal incisor microwear study was completed by Ryan (1980), in which he found gouging features similar to those found on the Ipiutak comparative sample. This was interpreted as an indication of the power-grasping and clamping activities of the anterior dentition in the Ipiutak, and was inferred behavior for the Neandertal sample (Ryan, 1980). This is in agreement with the present analyses, as the

cold-open-steppe Neandertals demonstrated a microwear signature most closely resembling that of the Ipiutak, which was interpreted as a heavy regimen of clamping and grasping activities.

Labial studies of the Krapina Neandertals were also completed, and found two types of labial striations: those that were closest to the incisal edge and larger ones on the central labial surface (Lalueza Fox & Frayer, 1997). While those on the incisal edge were attributed to grasping activities, those on the central labial surface were suggested to signify cutmarks from stone tools in a "stuff and cut" scenario (Lalueza Fox & Frayer, 1997).

The Krapina Neandertals were re-examined here using texture analysis, and evidence was found for non-dietary anterior tooth use behaviors. Interestingly, the Krapina Neandertals, dated to the last interglacial (OIS 5e), were closest in microwear textures to the Prince Rupert Harbour sample from British Columbia. This bioarchaeological sample used their anterior dentition to soften fibers for basketry tasks. While it is not suggested that the Krapina Neandertals were weaving baskets, it is suggested that their non-dietary anterior tooth use was not as intense or did not include as much high magnitude loading as that of the cold-open-steppe individuals.

Future research avenues

This research documented the effects of different variables and factors on Neandertal anterior tooth wear, and provided a large comparative modern human baseline, as well as a sizeable collection of anatomically modern human signals to use in future studies. This research could continue in several ways, including the addition of more Neandertal anterior dental textures to maintain the present interpretations. In

particular, a more substantial sample size of Neandertals and AMH from OIS 3 would allow for more concrete analyses of adaptive and behavioral differences during the Middle-to-Upper Paleolithic transition. Moreover, the inclusion of Neandertal and AMH subadults, from which anterior dental microwear textures from several individuals have already been collected, would permit differences in behavioral strategies by age to be examined. Regardless of the direction, Neandertal dietary and behavioral strategies are far from being completely recognized and understood; however, this project has taken substantial steps in acknowledging variation in this unique hominin's behavioral repertoire.

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